Beyond Fishing In the Newfoundland and Labrador Marine Shelf Ecosystem: The Roles of Climate and Environment in Affecting Change

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Abstract

The primary objective of this thesis is to identify and investigate important climatic and bottom-up processes affecting the marine shelf ecosystem off southern Labrador and eastern Newfoundland (Northwest Atlantic Fisheries Organization Divisions 2J3KLNO). The analyses are intended to extend the breadth of understanding for important ecosystem processes beyond the well-established impacts from overfishing. Knowledge gained from research on key commercial species is intended to address how ecological phenomena have affected the fisheries in recent decades and may be driving present changes in the ecosystem. Apart from advancing and informing science, the information presented is intended to benefit a wide audience of industry stakeholders including governments, harvesters, processors, and environmental interest groups.

Four research chapters are chronologically themed from the collapse of northern cod (*Gadus morhua*) in the late 1980s / early 1990s, to the delayed recovery of capelin (*Mallotus villosus*) and cod, to factors presently affecting the decline of snow crab (*Chionoecetes opilio*). The first two research chapters examine the impacts of temperature and diet in affecting physiological growth and performance of juvenile and adult northern cod during and following stock collapse. The third research chapter focuses on factors affecting the low abundance of capelin since an abrupt decline in the early 1990s, while the final research chapter reviews top-down and bottom-up processes contributing to the rise and fall of snow crab. Collectively, these works contribute to improved understanding of some of the most important ecosystem processes influencing Newfoundland and Labrador fisheries.

Temperature and food limitation were found to have a large impact on the Newfoundland and Labrador marine shelf ecosystem. Both factors either directly or indirectly regulated the productivity of each examined species. Recent warming coupled with increases in zooplankton abundance and an improving match between capelin spawning times and the spring bloom are shown to be supporting increasing abundances of capelin and by extension cod. Meanwhile, warming has directly led to a decline in snow crab productivity. Overall, the results suggest the Newfoundland and Labrador Shelf ecosystem is experiencing a shift in structure and forcing from being predominately bottom-up over the past two decades to a more balanced state wherein both bottom-up and top-down forcing are prevalent. To address concerns of management, advice based on the present findings is provided and putative future directions of the ecosystem, fisheries, and climate are discussed.

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The number of people to thank for the various individual research projects contained in this thesis are too numerous to mention here. Specific acknowledgements are provided in the research chapters.

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Table of Contents

List of Tables

List of Figures

Chapter 1

Introduction

1.1 Study Approach and Context

A key goal of this research was to better understand fish stocks and productivity along the Newfoundland and Labrador (NL) continental shelves. The works contained in the suite of research studies presented in this thesis focus on important historical and present fishery resources of eastern Newfoundland and southern Labrador. The Introduction briefly elaborates on the socio-economic ties of the people of the region to the fishery as well as debate in the scientific literature over what caused unprecedented finfish stock collapses in the early 1990s. The Introduction then transitions to contextually stage the principles and implications of the forthcoming research within the premises of trophic ecosystem control and ecosystem-based fisheries management. Collectively, four independent research works identify and investigate avenues by which climate and low trophic level processes affect the fisheries resources. Chronologically, the research chapters are presented and themed beginning with the collapse of the northern cod (*Gadus morhua*) in the early 1990s, transitioning to factors belabouring the recovery of cod and capelin (*Mallotus villosus*), and finishing with factors affecting the basis of the present mainstay fishery, snow crab (*Chionoecetes opilio*).

Change is a constant and fundamental feature of all ecosystems and can be caused by both natural and anthropogenic processes (Walker et al., 2004). Well documented and extreme changes have occurred along the Newfoundland and Labrador (NL) shelf ecosystem, but perhaps the most radical changes have occurred in the fisheries of recent decades (Rose, 2007). Changing environments along with competing objectives among stakeholder groups render fisheries difficult to manage (Hilborn, 2007). In NL, instability in both socio-economic and ecological realms renders the fishery a difficult industry for governments to establish effective long-term management and policy strategies or for harvesters and processors trying to undertake long-term planning (Schrank, 2005; Murray et al., 2006).

Although prediction of future changes in marine shelf ecosystems and fisheries is always uncertain, an underlying intent of this thesis is to provide guidance to managers and industry stakeholders on the current and anticipated near-future state of some of the main commercial species available to the NL fisheries. To do so, the primary objective is to identify and investigate important ecological processes affecting the 'NL Shelf' (Northwest Atlantic Fisheries Organization Divisions 2J3KLNO [Figures 1.1-1.2]). Knowledge gleaned will contribute to improved understanding of why events of recent decades occurred and provide a basis for anticipating forthcoming changes in community composition. It is hoped this knowledge will be of benefit to all industry sectors, in particular government departments such as Fisheries and Oceans Canada (DFO) that are currently seeking to establish an ecosystem-based approach, as opposed to single-species approaches, as the basis for management of marine resources (http://www.dfo-mpo.gc.ca/science/ecosystem).

The majority of analyses presented focus on climate and bottom-up ecosystem processes (nourishment, energetics). This approach intentionally avoids an in-depth examination of the well documented impacts of overfishing that have been widely accepted by science and industry stakeholders as important drivers affecting fish stocks along the NL shelf (Myers et al., 1996; 1997; Hutchings, 2004; Rice, 2006; Rose, 2007; Lilly, 2008; Etchegary, 2013).

The NL Shelf provides opportunities to study both top-down (fishing, predation) and bottom-up ecosystem processes. Its massive expanse encompasses contrasts in bathymetry (Figure 1.1) and temperature characteristics. While surface waters are generally cooler in the north and warmer in the south, bottom temperature gradients differ with the dominant shallow cold plateaus of the southern divisions (Div. 3LNO) contrasting the deep warm trenches characterizing much of the northern divisions (Div. 2J3K) (Figure 1.2). Along with dynamic physical and oceanographic features, the scale of rise and collapse of fish stocks that has occurred over time in this ecosystem is large, creating strong temporal contrast for studying fish population dynamics.

1.2 The Fishery and the People

Newfoundland was the first place in North America occupied by European settlement yet it is one of the least populated areas of the continent. Simply, it can be a harsh land. For 500 years from Newfoundland's humble beginnings as a European fishing outpost in the late 1400s and throughout most of its history, one industry formed the socio-economic fabric of the people - cod fishing (Sider, 2003; Etchegary, 2013). The cod (*Gadus morhua*) stocks here were historically among the world's largest and supported not only Newfoundlanders but peoples

throughout the world. However, beginning in the 1960s, and amplified in the early 1990s, unprecedented stock collapses occurred (Rose, 2007), creating significant changes not only in the fisheries but also in the way of life of the people (http://www.heritage.nf.ca/articles/economy/moratorium.php).

July 2, 1992, the day the Canadian Government imposed a moratorium on fishing the northern cod stock (Divisions 2J3KL), was arguably one of the bleakest in Newfoundland's history. Within two years all cod and most finfish stocks in the region were under moratoria. Overfishing by domestic and foreign fleets was widely touted as the cause (Myers et al., 1996; 1997; Hutchings, 2004; Shelton et al. 2006), although DFO management cited poor environmental conditions and suggested that the moratoria would be short-term and fishing would likely resume within a few years (https://www.cdli.ca/cod/announce.htm). However, some scientists predicted that rebuilding would take decades and distribution shifts would result in poor recruitment (deYoung and Rose, 1993). The predictions of deYoung and Rose (1993) have been borne out, and nearly 25 years since the collapse the moratoria persist and for the first time a generation of Newfoundlanders has been raised who know little about 'codfish'. However, there is currently converging anecdotal and scientific evidence to suggest that some cod stocks, including the northern cod, are rebuilding (DFO, 2014; Rose and Rowe, 2015).

During the period of upheaval following the collapse of cod and other finfish stocks, a seemingly minor decision by DFO to change its standard survey trawl to a smaller footgear and mesh configuration in 1995 (Walsh and McCallum, 1995), in an attempt to capture more juvenile fish for fisheries resource assessments (personal communication, Barry McCallum, DFO), would have unforeseen consequences on the fishery. Unexpectedly, northern shrimp

(*Pandalus borealis*) and snow crab started showing up in survey catches in high abundance (Orr and Sullivan, 2014; Mullowney et al., 2015). Within a few years, for those still fishing, a new basis for the industry had emerged and by the early 2000s Newfoundlanders were prosecuting the world's largest fisheries for these species and the industry was enjoying record profits (http://www.fishaq.gov.nl.ca/stats/; http://www.heritage.nf.ca/articles/economy/moratorium-impacts.php). Although there were ultimately fewer people involved in the fishery after the finfish collapses, with nearly 3,500 licences issued (Mullowney et al., 2015), the small-boat crab fishery in particular became the socio-economic mainstay of many fishing communities ('outports') (Hamilton and Butler, 2001; Schrank, 2005).

The volume of scientific papers focused on causes for the collapse and slow recovery of cod is large and the list of factors advanced as having either directly or indirectly contributed to its demise and slow rebuilding is extensive. Among the causes advanced by scientists as being either primary or highly influential factors were overfishing (Myers and Cadigan, 1995), rapid genetic evolution (Olsen et al., 2004; Hutchings, 2004), a cold oceanographic regime (Colbourne and Anderson, 2003), and diet deficiencies stemming from a lack of capelin (Rose and O'Driscoll, 2002). In a recent review, Lilly (2008) summarized that a confluence of high fishing mortality, partially attributable to an overestimation of stock size, ineffective management decisions following initial warnings, and changes in oceanographic conditions coincided to cause the collapse.

Circumstances similar to those facing the fishing industry during the groundfish collapse are at present re-emerging as the shrimp and crab resources are in decline (Orr and Sullivan, 2014;

Mullowney et al., 2015). Reduced quotas in these fisheries are making viability in the industry increasingly challenging for many harvesters (Personal communication, Annette Rumbolt, DFO resource manager). Meanwhile, some harvesters are experiencing catch rates near all-time highs in both the shrimp and crab fisheries (Orr and Sullivan, 2014; Mullowney et al., 2015). Recent scientific papers have discussed topics such as warming waters (Colbourne et al., 2013), changing productivity (DFO, 2014), and 'regime shifts' (Buren et al., 2014) as potential causes for the resource declines, but at the same time long and cold winters and extreme ice conditions (https://www.ec.gc.ca/glaces-ice/) have occurred in recent years. Understandably, the situation could be confusing to managers and industry.

The overall objectives of this thesis were to advance knowledge on why the cod collapsed, what has prolonged cod and capelin recovery, and what caused the rise and now decline of snow crab. The analyses explicitly focus on bottom-up and ecological processes as it is felt they may have been under-estimated in relation to the more thoroughly advanced and documented outcomes of overfishing during recent decades. In doing so, a complex suite of ecosystem survey data has been examined. Addressing questions on the basic mechanisms of the ecosystem and fish stock productivity was intended to assist implementation of an ecosystem-based approach to science and assessment, and ultimately fisheries management, and provide some clarity for industry on the future direction of the ecosystem and its fisheries.

1.3 Processes Associated with Stock Collapse

It is universally accepted that overfishing was instrumental in the decline of cod (e.g., Myers et al., 1996; 1997; Hutchings, 2004; Shelton et al. 2006; Rice, 2006). Overfishing may be viewed as

occurring when harvests exceed recruitment or impede resource or ecosystem productivity (Murawski, 2000). Fishing can exert a strong and direct influence on fish stocks through reductions in older fish, spatial contraction of populations, potential loss of subpopulations, alteration of life history traits, and habitat damage (Kjesbu et al., 2014). For Atlantic cod, Hilborn and Litzinger (2009) concluded that for 13 of 18 stocks in the North Atlantic, no mechanism other than excessive fishing was required to explain poor recovery following collapses. However, the northern cod was not one of these stocks.

It is unlikely that fishing alone could have caused the sudden and abrupt decrease in productivity that occurred in the northern cod stock in the mid-1980s (Rothschild, 2007; Hilborn and Litzinger, 2009). Although excessive fishing exacerbated the rapid stock decline to very low abundance in the early 1990s (Rose, 2007), the productivity and distribution shifts were associated with a shift from a warm to cold phase along the NL shelf (Colbourne et al., 2013) (Figure 1.3).

The North Atlantic Oscillation (NAO) (Figure 1.4) is the major basin-scale forcing factor of inter-annual climate variability in the North Atlantic (Greene et al., 2013). It essentially measures the difference of sea level atmospheric pressure between Iceland ('Icelandic Low') and the subtropical Atlantic ('Azores High'). Its impacts occur through air temperatures, surface heat fluxes, deep ocean convection, and ocean circulation mechanisms. Alexander and Deser (1995) noted that the Labrador Sea temperature history reflected that of the NAO index at a one to two year lag. A strong positive NAO produces northwesterly winds across NL which delivers cold Arctic air and relatively cool, nutrient poor Sub-Arctic water onto the continental shelf

(Carscadden et al., 2001). The Labrador Current's offshore component normally runs colder and fresher during positive NAO (Petrie and Drinkwater, 1993). In contrast, negative NAO phases are associated with warmer and more saline conditions, plausibly explained by increased westward transport of Labrador Current slope water out of the region and a more direct influence of meteorological forcing on the water column (Petrie, 2007). Impacts of the NAO resonate beyond temperature and ocean current trajectories. For example, it can affect the strength of vertical water exchanges through upwelling and downwelling and ultimately water column stratification, nutrient availability, and ecosystem productivity (Martinez et al., 2016).

The NAO underwent an abrupt shift to a positive phase in 1989. Following the NAO shift, conditions quickly cooled, and by 1991 all broad-scale ocean climate indices were indicating that temperatures had plummeted on the NL shelf (Figure 1.3). The NAO remained in a strongly positive phase for all but brief intervals during 1989-1995, an unusually long stretch relative to historical observations dating back to 1950 (Figure 1.4).

Cod and other fishes are heterotherms in which energy allocation is affected by temperature. In cold conditions, although metabolism and physiological processes may slow, more of the total energy budget is required for somatic maintenance and less surplus energy is available for growth and reproduction (Morgan et al., 2010). For northern cod, the requirement of additional energy to support growth and reproduction during the cold period was associated with a sharp reduction in the biomass of capelin, the key conduit of energy from zooplankton to higher trophic levels and the most important prey of cod (Rose and O'Driscoll, 2002) (Figure 1.5).

The biomass and abundance estimates of northern cod declined from 1989-1991 and the instantaneous mortality rate increased (Figure 1.6). Management did respond, with quotas (Total Allowable Catches [TACs]) and landings gradually ratcheted down (Figure 1.6), but harvest decreases proved insufficient to prevent further stock decline. Misreporting and discarding in domestic fisheries and unreported catches of the foreign fleets likely resulted in underestimating removals during this period (Harris, 1999; Etchegary, 2003). In addition, the potential for natural mortality in the form of predation was also increasing, with harp seals (*Pagophilus groenlandicus*) steadily increasing in abundance (Figure 1.7). By 1992, the northern cod had collapsed. Most recent reviews of events occurring concomitant with stock collapse agree that no single factor can explain the decline that occurred in the early 1990s (Rice, 2006; Rose, 2007; Lilly, 2008).

Several key questions arise. Why did the cod stock not collapse in previous cold periods, such as 1983-1985 (Figure. 1.3) when an initial low productivity episode occurred (Rothschild, 2007; Hilborn and Litzinger, 2009) and stock abundance and fishery landings were at similar levels (Figure 1.6); and, why have cod not recovered under low levels of fishing and warming conditions since the mid-1990s? It is noteworthy that capelin abundance remained strong during the mid-1980s cold period while it has been at very low levels since rapid decline over most of the range of the northern cod in the early 1990s (Buren et al., 2014) (Figure. 1.5). It emerges that the linkage of cod and capelin is a key component of this ecosystem to study in understanding cod population dynamics.

1.4 Trophic Control

For the purpose of this research, bottom-up and top-down forces are viewed as in classical ecology, with bottom-up forces referring to nutrient availability and top-down forces to predation (Hunter and Price, 1992). By extension, fishing is viewed as a top-down force. Climate processes strongly affect primary and secondary production in the marine ecosystem, and although climate variables themselves are not classical bottom-up forces, their impacts on the foodweb are viewed as bottom-up forces in these analyses. An ecosystem driver is defined as any natural or human-induced factor that directly or indirectly causes a change in an ecosystem (Nelson et al., 2006). A forcing is an analogous term.

In the system of fisheries management practiced in Canada and most other countries with advanced management systems, quota regulation is employed. Thus, by default, the focus is on fishery exploitation with bottom-up factors not normally explicitly considered in harvest advice. Nonetheless, most fisheries scientists understand that neither bottom-up or top-down processes operate in isolation and complex interactions must be understood in order to assess and attempt to predict future resource status (Sissenwine, 1984; Link, 2002).

The traditional view of marine ecosystems is that they are food-limited and structured by bottom-up plankton control (Frank et al., 2007). Long advanced theories such as the Match-Mismatch Hypothesis (Cushing, 1969; 1990) and Stable Oceans Hypothesis (Lasker, 1981) hold that predators are highly dependent on establishing close spatiotemporal associations with prey. In particular, phenological events at low trophic levels are critical, with first-feeding stages of forage fishes and larval emergence timed to coincide with primary and secondary production

from plankton blooms, although bottlenecks at older life stages can also occur, such as skipped spawning in adult females of species capable of spawning in multiple years (Rideout and Rose, 2006) or increased mortality in juveniles or adults (Brattey et al., 2010).

Temperature and related climate phenomena such as sea ice are important forcing mechanisms affecting the dynamics of primary and secondary production (Wu et al. 2007; Buren et al., 2014). Accordingly, climate effects can directly affect energy production at the base levels of foodwebs and are strongly linked to bottom-up regulation of communities. Temperature in particular can directly, indirectly, or synergistically influence community structure in marine ecosystems throughout the Northern Hemisphere (Boyce et al., 2015). However, in cold regions such as the NL shelf top-down controls, be they natural or anthropogenic, often structure community composition (Frank et al., 2006; Petrie et al., 2009). These northern marine ecosystems often feature low species diversity with compensatory food web dynamics limited. With low resilience to fishing relative to more diverse ecosystems, excessive removals of top predators can lead to 'trophic cascades', which are broad-scale and elicit rapid systematic changes throughout the foodweb in response to the loss of top predators (Frank et al., 2005; 2006; 2007).

Trophic controls change even in the absence of fishing, consistent with temperature being a constant determinant of ecosystem structure (Boyce et al., 2015). As climate imposes directional forcings an ecosystem can respond with a pattern of oscillating trophic control, invoking alternation between top-down and bottom-up dominance. Ecosystems in which fishing occurs can also undergo trophic oscillations (Hunt et al., 2002; 2011; Litzow and Cianelli,

2007). For example, a rapid warming in the Gulf of Alaska in the 1970s caused an oscillation from a bottom-up to a top-down structured ecosystem, shifting from a community dominated by small pelagics to one dominated by large predatory groundfish species (Anderson and Piatt, 1999; Litzow and Cianelli, 2007). Similarly, in the North Atlantic, a prolonged warming in the 1920-1930s that persisted into the 1950-1960s resulted in a general northward movement of temperate species and high recruitment of large predatory groundfishes (Drinkwater, 2006). These changes in dominant trophic control are often referred to as regime shifts, generally understood to mean climate-forced reorganizations of ecosystems from one relatively stable state to another (Anderson and Piatt, 1999; Drinkwater, 2006).

Broadly, the hypothesis of this thesis is that the NL shelf has been under strong bottom-up control since the early 1990s, with food limitation inhibiting recovery of pelagic forage fishes and apex predators. Support for that hypothesis requires evidence of food limitation or bottom-up control (as defined earlier) in what are believed to be key species in this ecosystem, namely capelin, snow crab, and Atlantic cod.

1.5 Ecosystem-Based Fisheries Management

Fishing is one of the few factors affecting fisheries resources that can be directly controlled by management. Generally, fisheries management in Canada and most developed countries focuses on trying to control spatiotemporal patterns of fishing, fishing methods, and harvest levels. In Canada, fisheries management has historically and continues to be conducted at a

single-stock level, with habitat, functional role, and interactive processes in the ecosystem not explicitly considered in arriving at harvest level decisions for a given stock. Quantitative harvest strategies such as $F_{MSY,}$ the fishing exploitation rate that maximizes the sustainable yield from a fishery resource, are often employed in formulating management advice. Such approaches have contributed to a situation where globally about 90 % of fished stocks are over- or fully-exploited (FAO, 2012). Even emerging management approaches such as Precautionary Approach reference points and complementary harvest control rules (Caddy and McGarvey, 1996; Hutchings, 2000) continue to generally feature biomass- or exploitation-based targets at the single-stock level.

The notion of an ecosystem-based fisheries management (EBFM) system is not novel, having long been viewed by ecologists as a best approach for management of marine ecosystems (Slocombe, 1993). It is becoming increasingly accepted that F_{MSY} and similar approaches are far too simplistic in focus for proper management of fisheries resources. With recruitment in fish stocks broadly understood to be connected to environmental fluctuations and processes (Sissenwine, 1984), it is prudent to try to more formally incorporate environmental processes into resource management and planning (Link, 2002).

The Food and Agriculture Organization of the United Nations (FAO) defines an ecosystem approach to fisheries as one that strives to balance diverse societal objectives, by taking into account the knowledge and uncertainties about biotic, abiotic, and human components of ecosystems and their interactions and applying an integrated approach to fisheries within ecologically meaningful boundaries (FAO, 2003). Following this definition, to be achievable,

expertise must be combined from marine ecologists, fisheries scientists, oceanographers, and sociologists, among a host of other disciplines.

Presently, DFO is striving to implement an ecosystem-based framework into management of commercial fishery resources in Canada (http://www.dfo-mpo.gc.ca/science/ecosystem), including those along the NL Shelf. Recent initiatives such as the Ecosystem Research Indicators (ERI) (DFO, 2012a) and the Strategic Program for Ecosystem-Based Research and Advice (SPERA) (http://www.dfo-mpo.gc.ca/science/ecosystem/projects) are changing the focus of advice provided by DFO's Science Program by attempting to more holistically collect and incorporate data on ecosystem components beyond commercial species. Similar initiatives exist in other regions of the North Atlantic such as the Integrated Ecosystem Assessments (IEA) (http://www.ices.dk/Integrated-ecosystem-assessments.aspx) undertaken by European countries party to the International Council for Exploration of the Sea (ICES) and the management approach presently being advanced by the National Oceanographic and Atmospheric Administration (NOAA) in the United States (http://ecosystems.noaa.gov).

Despite such efforts by scientific institutions to advance EBFM, and the broad-based implementation of policies and frameworks by management bodies to promote it (Murawski, 2007), ecosystem-based advice is rarely explicitly incorporated into setting quotas, with the single-species approach still prevailing. For example, in Canada, the Sustainable Fisheries Framework of DFO (http://www.dfo-mpo.gc.ca) forms the foundation for implementing EBFM into management decisions via such emerging tools as the Precautionary Approach, which, paradoxically is applied at a single-stock level.

One obstacle to implementing EBFM in NL is that management area boundaries often do not conform to biologically meaningful units. For example, for the snow crab resource, there are nearly 50 small-scale management areas (Mullowney et al., 2015) while the resource constitutes a single panmitic stock surrounding not only the Province but extending throughout Atlantic Canada (Puebla et al. 2008; Mullowney et al., 2015). The small spatial scale of management reflects an attempt to segregate fishing grounds for various fleet sectors, with small vessels incapable of accessing the farthest offshore grounds and larger vessels prohibited from fishing inshore. Further, with a push toward co-management, harvesters have become an integral part of the decision making process at the management area level, thus the spatial scale of harvest level decisions does not fit the stock or even a meta-population scale and would likely be difficult to incorporate into an EBFM framework. Nonetheless, such inconsistencies should not be used as the basis to prohibit advancement of EBFM (Murawski, 2007).

Advocating for the concept of EBFM is proving easier than actually implementing it as the basis of fisheries management. Among the underlying challenges for scientists is to advance knowledge and methodologies to comprehensively combine information on the influences of bottom-up and top-down forces in understanding and predicting the trajectory or state of a given set of resources. Suites of broad-scale ecosystem modeling and comparative exercises such as those contained in journal theme sections like ‘Comparative analysis of marine fisheries production’ (MEPS 469, 2012) and the ‘Effects of climate and predation on subarctic crustacean populations’ (MEPS 459, 2012) have provided insight into the current status of knowledge and progress on establishing a scientific basis for EBFM in northern shelf ecosystems, but further

work on predicting how perturbation on one or multiple ecosystem components in time affects ecosystem functioning is necessary.

Climate and its impacts are especially difficult issues to deal with in establishing EBFM frameworks. The stochastic spatiotemporal patterns of change associated with most climate variables renders quantitative assessment difficult (Hasselman, 1975). These processes, difficult to understand, quantify, and predict as they may be, have resonating impacts throughout foodwebs through their effects on energy production and consequently species composition and abundances. The research works contained herein make a contribution to improving the understanding of impacts from climate-driven processes affecting foodweb dynamics and resources available to the fisheries of Newfoundland and Labrador, and thus directly apply to the principles of advancing EBFM in this region.

1.6 Co-authorship Statement

It is necessary to identify my role in fisheries science in Newfoundland and Labrador. I am employed by DFO NL Region in the capacity of subject matter expert and stock assessment lead for snow crab. While much of this work was physically undertaken at DFO, the views expressed on research outcomes herein are independent of DFO and solely my own.

I am the major intellectual contributor and principal author of all chapters presented in this thesis. Most of the data used consist of long time series' collected by DFO and other institutions such as Environment Canada (EC), the United States National Oceanic and Atmospheric Administration (NOAA), and the Sir Alister Hardy Foundation for Ocean Sciences (SAHFOS). Data

were also provided by my supervisors and committee members for various projects undertaken by DFO and Memorial University of Newfoundland (MUN). The work could not have been completed without collaborative efforts with my supervisors Drs. George Rose and Sherrylynn Rowe, work colleagues Gary Maillet and Eugene Colbourne, and committee member Earl Dawe. I prepared the manuscripts and revised them based on the advice and comments from my co-authors. Some figures used in the introduction and summary chapters were kindly provided by personnel at DFO with acknowledgements in figure captions.

Chapter 2. Mullowney, D., Rose, G., Rowe, S., Dawe, E., and Maillet, G. 'Temperature influences on growth and condition of inshore juvenile northern cod (*Gadus morhua*) during and following stock collapse' may be submitted for publication following completion of this degree.

Chapter 3. Mullowney, D.R.J., and Rose, G.A., 2014. 'Is recovery of northern cod limited by poor feeding: the capelin hypothesis revisited' has been published by ICES Journal of Marine Science; - 71: 784-793. Slight alterations have been made in the version presented here based on reviews of the thesis.

Chapter 4. Mullowney, D., Maillet, G., Dawe, E., Rose, G., and Rowe, S., 2016. 'Spawning delays of northern capelin (*Mallotus villosis*) and recovery dynamics: a mismatch with ice-mediated spring bloom?' was published in Progress in Oceanography; - 141: 144-152. Slight alterations have been made in the version presented here based on reviews of the thesis.

Chapter 5. Mullowney D.R.J., Dawe, E.G., Colbourne, E.B., and Rose, G.A., 2014. 'A review of factors contributing to the decline of Newfoundland and Labrador snow crab (*Chionoecetes*

opilio)' has been published in Reviews in Fish Biology and Fisheries – 24: 639-657. Again, slight alterations have been made in the version presented here based on reviews of the thesis.

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1.8 Figures

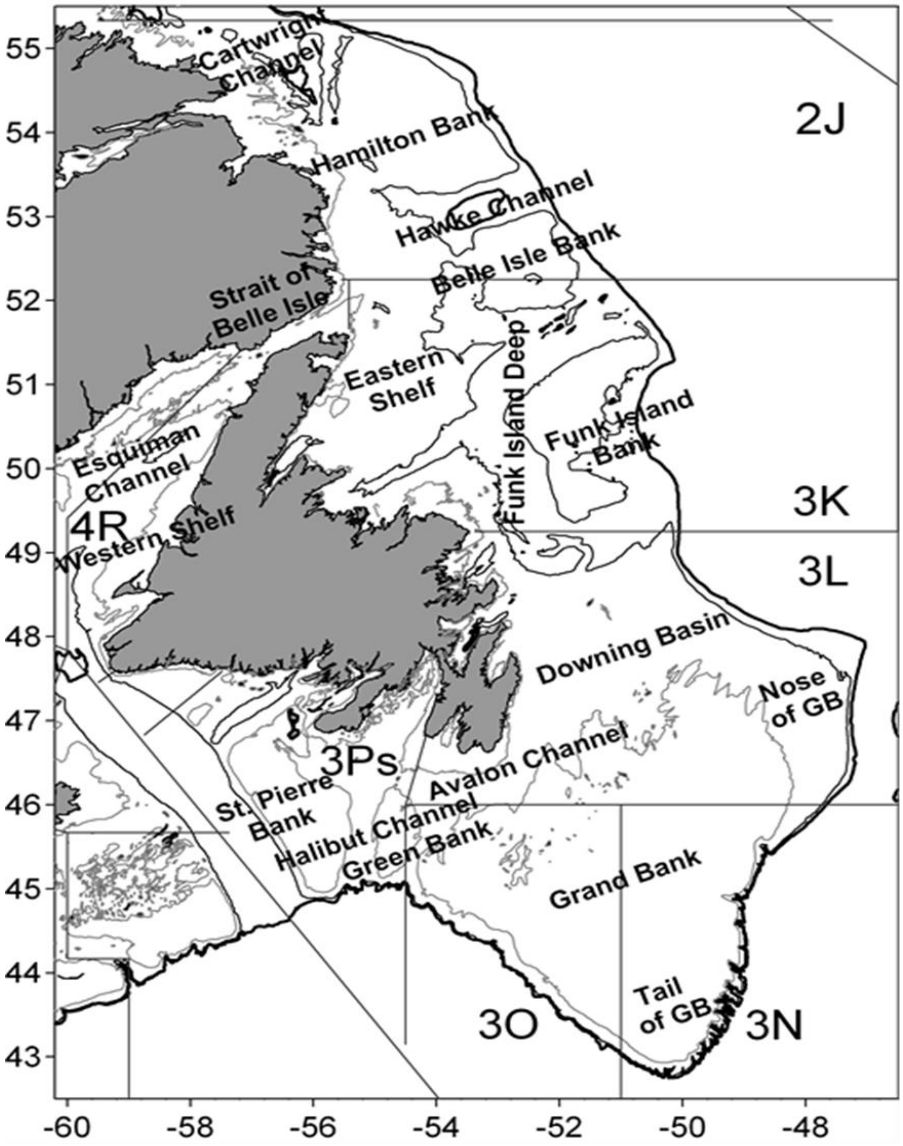

Figure 1.1. Map of the continental shelves surrounding Newfoundland and Labrador showing names of important bathymetric features as well as the Northwest Atlantic Fisheries Organization Divisions. 100m (grey), 300m (black) and 500m (thick black) depth contours shown.

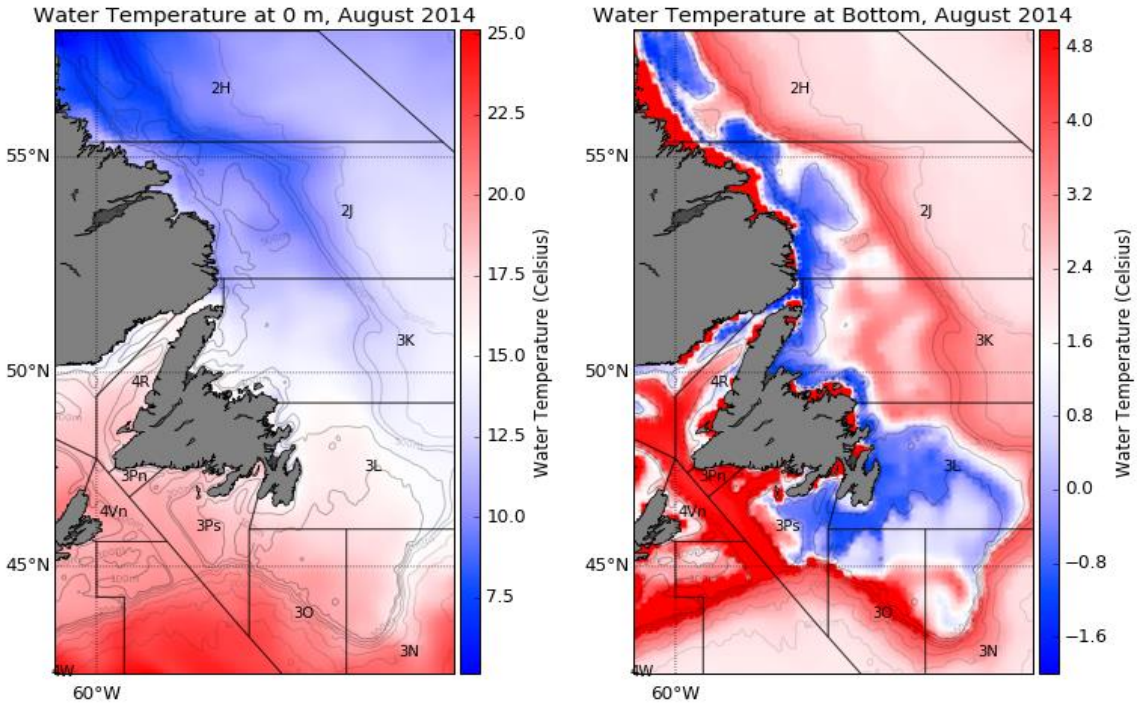

Figure 1.2. Maps of surface (left) and bottom (right) temperatures along and adjacent to the Newfoundland and Labrador shelf during August, 2014. Data acquired from the Global Ice-Ocean Prediction System (https://www.wmo.int/pages/prog/arep/wwrp/new/wwosc/documents/WWOSC2014_SURCEL_final.pdf)

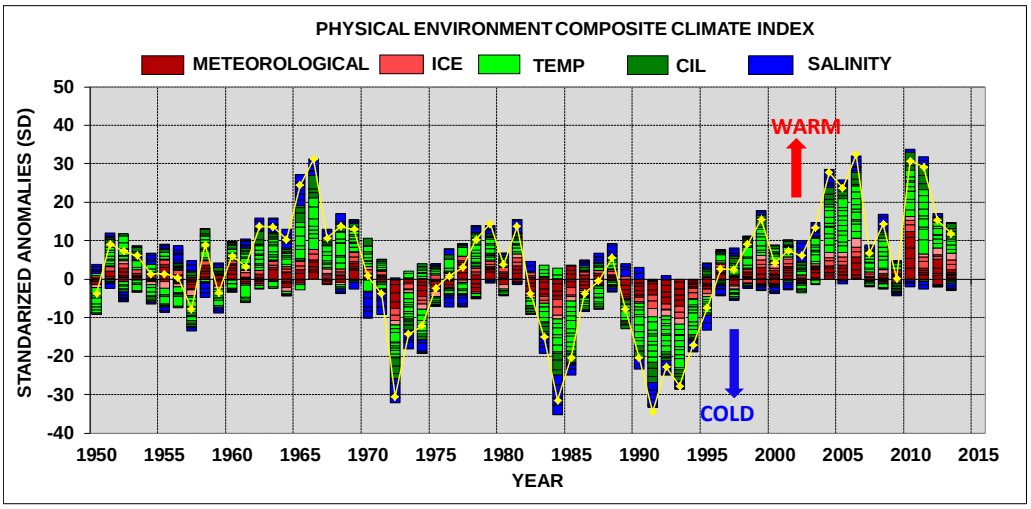

Figure. 1.3. Composite climate index derived by summing standardized anomalies of NAO, air temperature, ice, water temperature, and salinity and cold intermediate areas from several locations in the Northwest Atlantic. Anomalies were calculated from the 1981-2010 period. Figure taken from DFO, 2014.

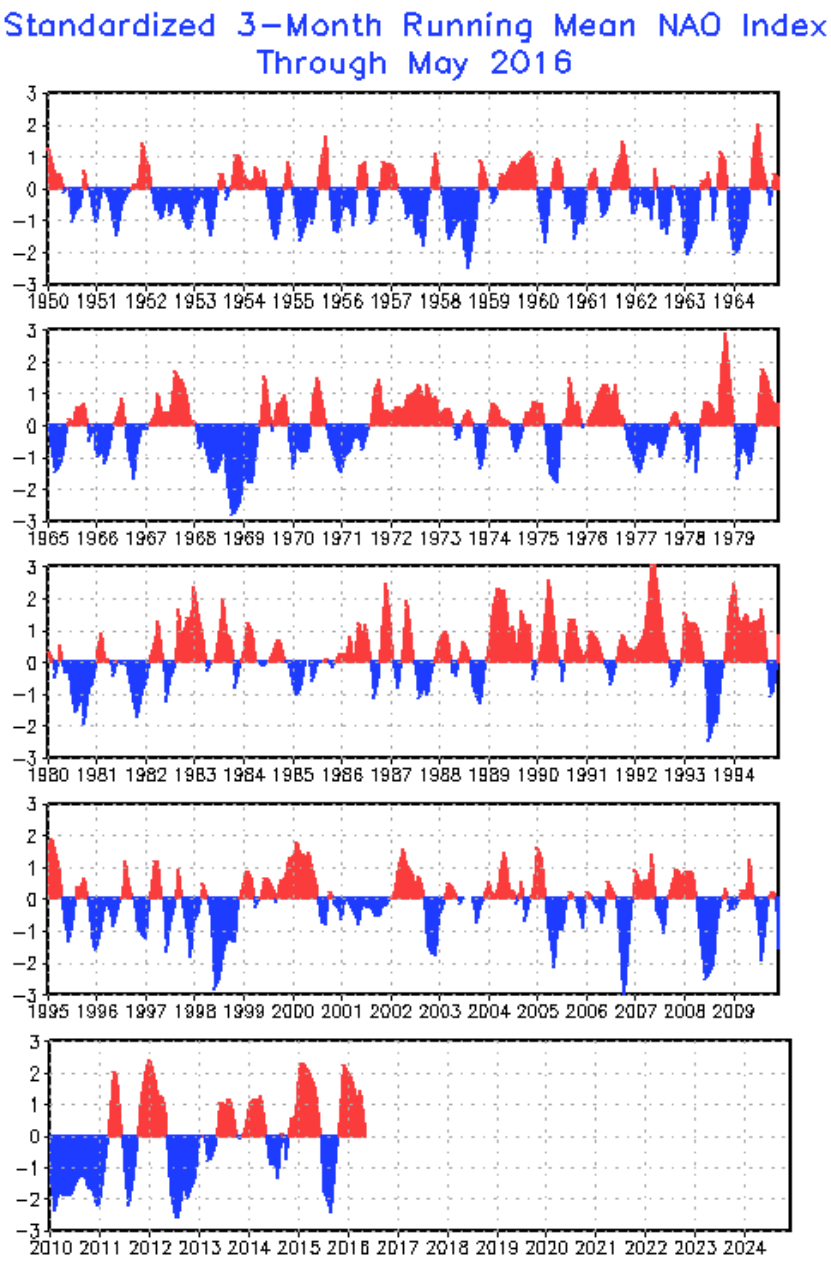

Figure 1.4. Standardized 3-month running mean of the North Atlantic Oscillation Index from 1950 to May 2016. Anomalies were calculated based on 1950-2000 period. Figure and calculation methods available from the United States National Oceanographic and Atmospheric Association webpage (http://www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/nao.shtml).

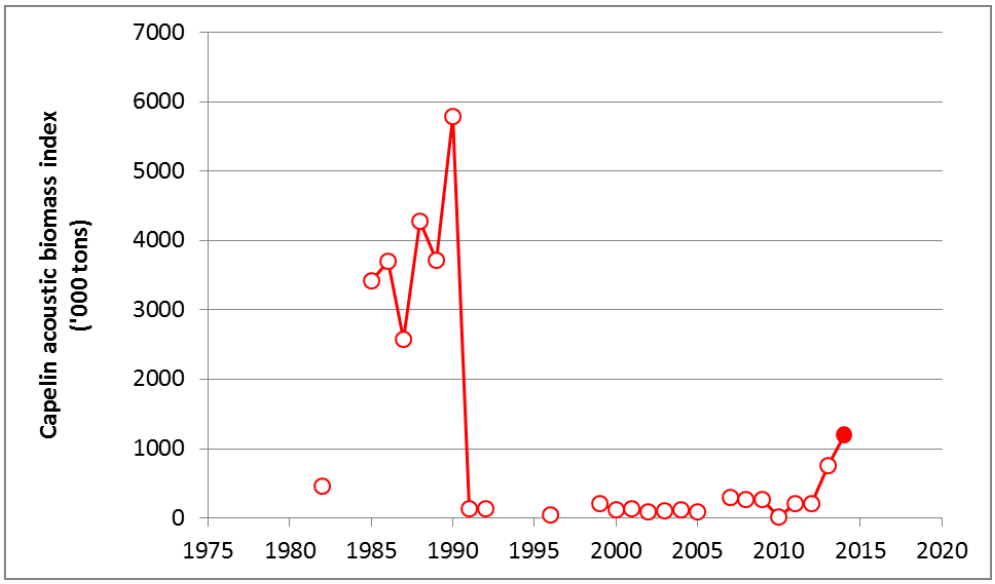

Figure. 1.5. Capelin Acoustic Biomass Index from the DFO spring capelin survey in NAFO Divisions 3KL. The 2014 point is preliminary. Figure taken from DFO, 2014.

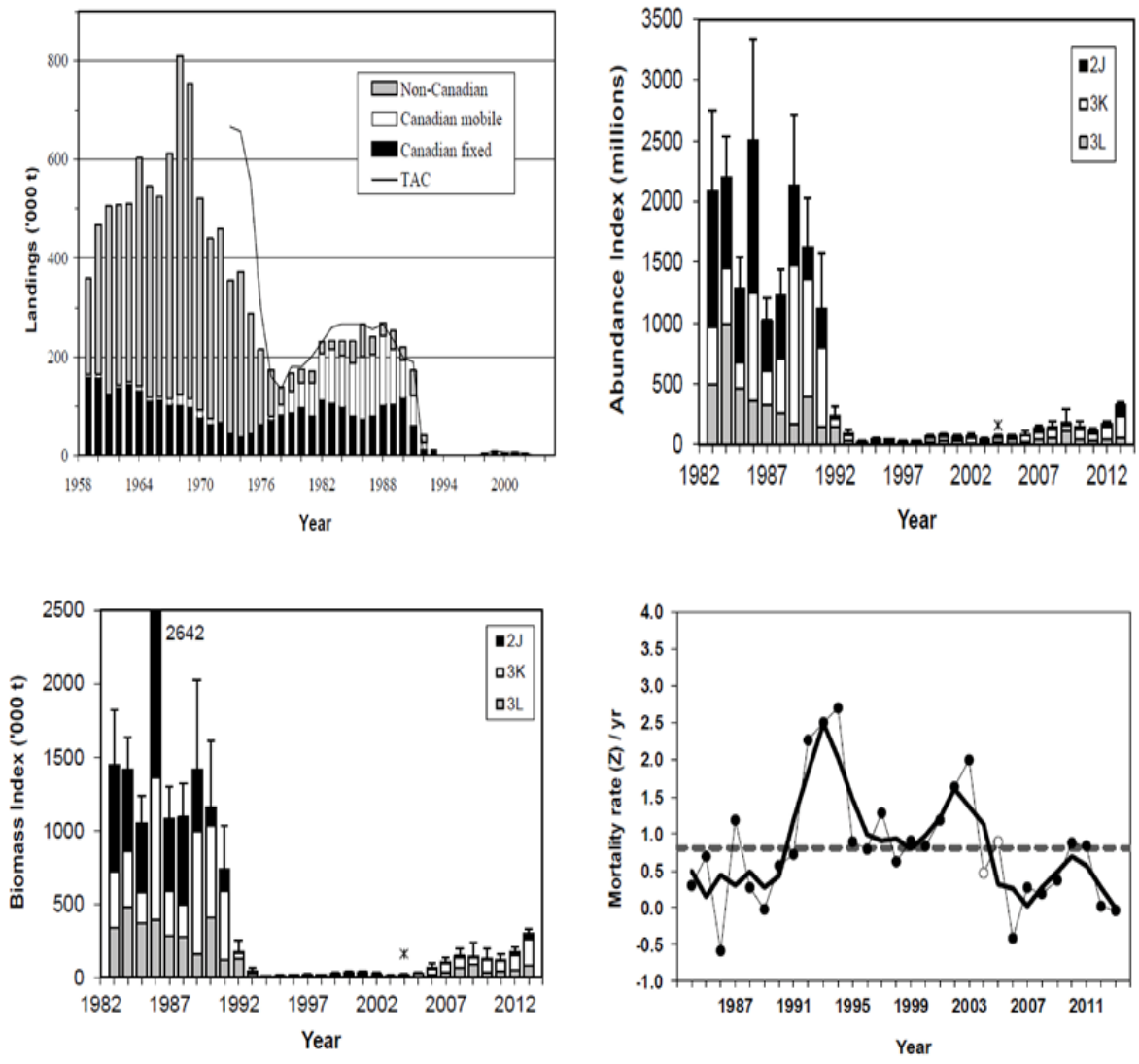

Figure 1.6. Northern Cod Total Allowable Catch and reported landings by Canadian and Non-Canadian fishing fleets (top left), abundance index by NAFO Division (top right), biomass index by NAFO Division (bottom left), and instantaneous mortality rate index [solid line shows two period moving average and dashed line shows annual estimates] (bottom right). (bottom right). Figure taken from (http://publications.gc.ca/Collection-R/LoPBdP/BP/bp313-e.htm#QUOTAS.)

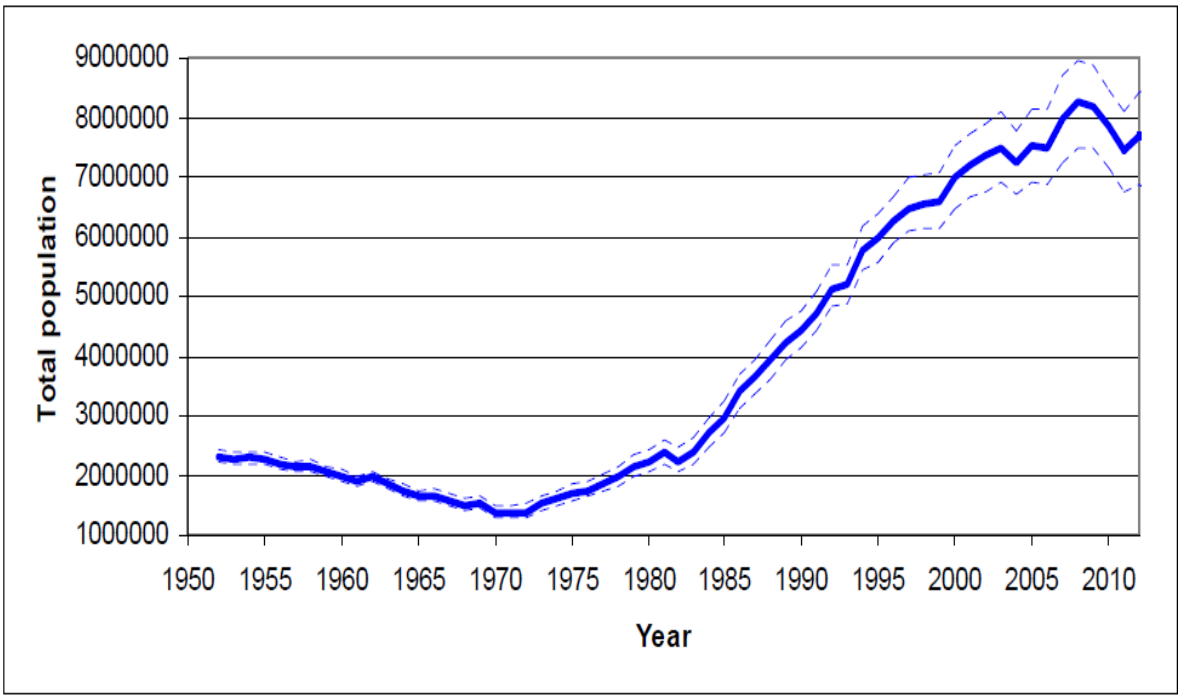

Figure 1.7. Estimated total population of Northwest Atlantic harp seals from 1952-2012. Figure taken from DFO, 2012b.

Chapter 2

Cumulative temperature influences on growth of inshore juvenile northern cod (*Gadus morhua*) during and following stock collapse

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Chapter 2 uses two previously unpublished datasets to examine growth performance of juvenile northern cod in relation to temperature during and following stock collapse. Although there is an abundance of literature on cod stock collapse, papers focused on juveniles are scarce or nil. The 'squid trap' series is the only known survey data on juvenile northern cod during stock collapse. Despite spatio-temporal inconsistencies in the data series', a major strength of the analysis is that a focus on juveniles allows for a relatively unbiased examination of environmental impacts on cod during stock collapse, with these fish being largely immune from fishing mortality. The study finds that growth was poor during the cold years associated with stock collapse but improved thereafter as temperatures increased. Chronologically and thematically, the chapter establishes that the collapse of cod was in-part attributable to climatic factors. It serves as a basis for continuing to build a case in forthcoming chapters that bottom-up factors were strong regulators of cod as well as other key species in the ecosystem both during and following stock collapse.

2.1 Abstract

This study examined growth performance of juvenile northern cod (ages 1-4) during and following stock collapse in the cold early 1990s. Two unpublished survey datasets were examined, one from squid traps at four sites on the northeast coast of Newfoundland (1991-1994) and the other from a trawl survey of an inshore site in Trinity Bay (1997-2004). Temperature was found to exert a strong effect on growth rates of juvenile northern cod, with year classes born during the cold stock collapse period experiencing slower growth than those born during the post-collapse warming period. The effect of temperature was cumulative, so that by age 4 the predicted length of the fastest growing 2001 year class was 13 cm and 35% longer than the slowest growing 1990 year class. The influences of temperature were spatially broad-based with no significant differences in early-life growth rates for year classes captured at sites spanning the entire length of Newfoundland's north and east coasts. It appears that reduced productivity during and following the collapse of this stock largely reflected environmentally-driven phenotypic responses to adverse environmental conditions and that subsequent warming has since promoted a prolonged period of improved growth and productivity.

2.2 Introduction

The collapse of the 'northern' cod is well known (i.e., Rose 2007), as is the preceding decline in productivity (Rothschild, 2007; Hilborn and Litzinger, 2009) that exacerbated overfishing of this stock in the 1980s and early 1990s (Hutchings, 1996; Myers et al., 1996). A key component of that productivity loss was reduced weight-at-age of adult fish (Dutil and Brander, 2003; Brander, 2007). Other studies have reported decreased growth and condition as abundance declined during the cold years of the early 1990s (Sherwood et al., 2007, Brattey et al., 2010). The growth and condition of juveniles during this cold period has not been thoroughly examined, however, likely because juveniles of ages 1-3 years were not typically fished and only minimally represented in survey data (Brattey et al., 2010).

Ambient temperature is known to affect growth rates in ectotherms in general (Neuheimer and Taggart, 2007). In cod, it affects growth rates at all stages from larvae (Pepin et al., 1995; Otterlei et al., 1999; Otterson et al., 2006) to juveniles and adults (Brander, 1994; Drinkwater, 2005) and likely explains much of the variation in individual growth evident among stocks (Purchase and Brown, 2000; 2001; Rose, 2007; Brander, 2007). Neuheimer and Taggart (2007) found that growing degree day differentials explained 93% of the variation in length at time for cod stocks across their distributional range. Increased temperatures have been shown to promote increased productivity in cod stocks throughout the north Atlantic (Dutil and Brander, 2003), although Drinkwater (2005) predicted recruitment in stocks at the southern end of their range would be poor under future warming scenarios. Nonetheless, general consensus is that the northern cod, which inhabits some of the coldest waters occurring across the species range and was historically among the slowest growing of all cod stocks (Brander, 1994; 1995), should

experience increased production and recruitment with warming. It follows that juveniles may have experienced reduced growth with cooling in the early 1990s, and if so, this would have likely reduced productivity and contributed to the lack of rebuilding that followed in the later 1990s.

The objective of this study was to examine the hypothesis that growth of juvenile northern cod was lower in the cold period in the early 1990s than in the warmer post-collapse years. To test this hypothesis, previously unpublished data from cod captured in squid traps set in four locations along the northeast coast of Newfoundland during the cold 1991-1994 stock collapse period were compared with trawl captured samples taken from Smith Sound in inner Trinity Bay during a 1997-2003 post-collapse warming period.

2.3 Methods

2.3.1 Fish Growth

'Squid traps' (Japanese pelagic traps) were set along the northeast Newfoundland coast during 1991-1994 to capture juvenile northern cod samples for assessment of biophysical attributes in the period coinciding with stock collapse. Individual traps were set at four locations: St. Lunaire on the Northern Peninsula, Herring Neck in Notre Dame Bay, Bellevue in Trinity Bay, and Holyrood in Conception Bay (Figure 2.1). The traps were similar in configuration to a traditional Newfoundland cod trap, featuring a floating small-meshed box with a large-meshed leader approximately 30m in length extending from sea surface to bottom and perpendicular from shore to the box opening ('door'). A mesh ramp extended from the floor of the box to guide

fish toward the door. Wings extended at 45 degree angles from the shoreward corners of the box to complement the leader in guiding fish toward the door.

Traps were set near shore at depths of about 10-13 m. For each individual captured, total length was measured to the nearest centimetre and sex and maturity status determined by visual observation of the gonad (Templeman et al., 1978). Otoliths were collected randomly from sampled fish and ages estimated by trained individuals at the Department of Fisheries and Oceans (DFO) Northwest Atlantic Fisheries Centre in St. John's, Newfoundland, using standard procedures.

The data collection design was not balanced insofar as not all sites were occupied each year and annual sampling periods and duration differed both within and across sites (Table 2.1). There was no sampling at St. Lunaire in 1991 and 1994, Herring Neck in 1991, and Bellevue in 1994. In the two years St. Lunaire was visited, most samples were taken from July to October, while samples from Herring Neck were generally taken earlier, predominately from June to September. Bellevue and Holyrood tended to be occupied later, with most samples taken during late summer or early fall. Although it is difficult to control for such spatiotemporal bias in quantitative analyses, they are important to consider in interpretation and qualitative assessment of growth. To partially control for the bias, fish length data were restricted to June to September.

The squid traps consistently captured fish ranging in ages 1-4 years. Initial analyses revealed that virtually all fish were immature and there were no differences in sex- or maturity-specific lengths, thus all data were pooled to age regardless of sex or maturity. To focus on growth over

time, fish captured at each location were segregated into year classes. To test for differences in growth across sites, length data were natural log-transformed and examined in a general linear model (GLM), regressing the dependent length variable against the main and interaction effects of age, year class, and location, all of which were treated as class variables. Type IV sum of squares was used in the model to control for missing cells (i.e. not all locations sampled each year) in the statistical design.

Cod were caught in Smith Sound, Trinity Bay (Figure 2.1) from 1998-2004 during surveys conducted in winter (mid-January) from the Canadian Coast Guard research trawler *Teleost*, utilizing a Campelen 1800 shrimp trawl equipped with 18" rockhopper footgear. These surveys were not specifically targeted at juveniles; rather, they functioned to monitor status of the entire cod population in Smith Sound, the sole known large aggregation of northern cod to persist in the post-collapse period inshore. Survey tows were conducted for 15 min. duration at 3 knots, with lengths and otoliths taken from all sampled fish (Table 2.2; See Rose, 2003 for further details). For comparison with the squid trap samples, data from the Smith Sound surveys were limited to fish ages 1-4 years. Males and females did not differ significantly in length over this age range and the Smith Sound fish were segregated into year classes in analogous fashion to the squid trap samples, with fish initially pooled to age regardless of sex.

Sizes-at-age for each year class were compared between the two survey series, with locations in the squid trap survey pooled due to a lack of significance in length differences across locations. For year classes that were captured over a minimum of three years in the respective surveys, linear regression growth curves were fit to size-at-age data, with the growth curves

forced through the origin. Linear regression was used in lieu of more conventional asymptotic-type curves such as von Bertalanffy growth models because there were no indications of asymptotic limits of maximum size being approached at these young ages. The slopes (M) of the growth curves were used to calculate predicted length-at-age for each year class.

2.3.2 Temperature

Near-surface temperatures were recorded at most sites and years during the squid trap surveys using thermographs placed on the upper portions of the traps (no temperature data were acquired during 1994 at Holyrood). These data were deemed too spatially and temporally limited to capture a broad-scale signal of temperature that would have influenced growth of fish captured in the study. To broaden the spatiotemporal scope, sea surface temperature data from standard oceanographic monitoring sites termed 'Petrie Boxes' in offshore regions of the shelf (Figure 2.1) were utilized. These data originated from the *Pathfinder 5.2* satellite system (http://www.nodc.noaa.gov) and were compiled by the Oceanography Section at the Bedford Institute of Oceanography in Dartmouth, Nova Scotia (Figure 1; see Colbourne et al., 2012 for further details). Surface temperatures were used in lieu of bottom temperature as no known continuous broad-scale records of bottom temperature existed. Temperature data from satellite systems were exclusive to the surface. To validate the reliability of offshore Petrie Box data as a proxy for temperatures occurring in inshore areas where fish were captured, monthly mean temperatures from squid traps were compared with those from the closest adjacent Petrie Box (St. Lunaire = St. Anthony Basin, Herring Neck = Northeast Shelf, Bellevue & Holyrood = Avalon Channel) using simple linear regression.

An index of temperature experienced throughout life for each year class was developed from the Petrie Box sea surface temperature data. Initially, an average of monthly temperatures from the St. Anthony Basin, Northeast Shelf, and Avalon Channel boxes was calculated to capture a broad spatial scale of ambient temperature. These monthly averages were then summed to develop a broad temporal index of temperatures occurring each year. This index is somewhat analogous to the more conventional growing degree day (GDD) concept applied in ecological sciences (Neuheimer and Taggart, 2007). However, our coarse-grain data did not allow us to track daily temperatures over the study period (monthly bins used) and we did not have a reliable basis for estimating a base temperature from which to measure deviations. The annual index of cumulative temperatures was additively applied to cod of each year class at any given age. For example, for the 1990 year class, a one year old fish captured in 1991 would have experienced the cumulative sum of 1990 (at age 0) and 1991 (at age 1) temperatures, while a two year old fish from the 1990 year class captured in 1992 would have experienced the cumulative sum of 1990-1992 temperatures.

Finally, the sum of temperature-at-age index was compared to growth rates slopes for each year class using simple linear regression to assess cumulative effects of temperature in regulating fish size, and incorporated into a GLM testing the direct and interactive effects of age and cumulative temperature in affecting growth. The dependent variable in the model was natural log-transformed length-at-age for each year class, and cumulative temperature was treated as a continuous explanatory variable.

2.4 Results

2.4.1 Fish Growth

There was no difference in growth rates across locations in the squid trap survey series. The GLM showed location to be non-significant both as a main effect (*f=0.56, p=0.6621*) and in interactions with age (*f=1.91, p=0.2456*) and year class (*f=0.94, p=0.58*) in affecting fish length (Table 2.3). There were significant differences in length across ages and year classes, both as main and interaction effects.

Residuals from growth models were small and showed no directional pattern for most year classes (Table 2.4). There appeared some systematic under-estimation of predicted sizes in age 2 and especially age 1 fish, however, in the 1989-1991 squid trap data year classes (Figure 2.2; Table 2.4). This is likely a function of the later sampling and associated longer growth increment from birth to first measurement that occurred in this data series compared to Smith Sound, and process error introduced by forcing the regression curves through the origin. Nonetheless, model fits for the older ages appeared to sufficiently correspond with observed length values. The lowest growth rate slopes occurred in the 1989-1991 year classes (M=9.43-9.61). These slow growing year classes achieved observed and predicted sizes of about 35-38 cm total length by age 4. During the post-collapse period, growth rates initially decreased slightly from M=10.71 in 1996 to M=10.43 in 1998, but increased relatively rapidly thereafter to M=12.71 in the 2001 year class. From 1996-1998, fish consistently achieved observed and predicted lengths of 41-42cm by age 4. From 1999-2001, length at age 4 had increased markedly to 42-43 cm in

1999 and almost 51 cm in 2001. The predicted size of 50.9 cm at age 4 in the fastest growing 2001 year class was 13.2 cm larger than the slowest growing 1990 year class, a 35% difference.

2.4.2 Temperature

Shoreline temperatures at squid trap survey sites all showed significant ($p<0.05$) positive relationships with the broader signals of continuous offshore sea surface temperature data collections from adjacent Petrie Boxes (Figure 2.3). Accordingly, Petrie Box temperatures were deemed a reliable proxy for inshore temperatures, although it was recognized that regression slope intercepts indicated shoreline temperatures were overall slightly higher than in the offshore. Sea surface temperatures were lowest in the early 1990s and showed an increasing and oscillating pattern thereafter (Figure 2.4). The slow growing 1989-1991 year classes experienced the lowest ambient temperatures up to age 4 while the fast growing 2000-2001 year classes experienced the highest ambient conditions (Figure 2.4, Table 2.4). The cumulative temperatures experienced to age 4 for the coldest 1989 year class (Index=198.82) was 16 % lower than that experienced by the warmest 2001 year class (Index=229.54).

The effect of temperature on growth rates was significant ($p<0.05$) at all ages except age 1 (Table 2.5). These relationships grew stronger and more highly significant with age (Figure 2.5, Table 2.5). The general patterns of stronger significance and tighter correlations in the age 3 and 4 year classes coupled with increasing slopes of the regression curves (M=.086 at age 3 and 4 versus M=.058-.067 at age 1 and 2) demonstrates that the effects of temperature on fish growth are cumulative.

The effect of cumulative temperature on fish length was significant both as a main effect (*f=2.97, p=0.0147*) and as an interaction with age (*f=6.16, p=0.0033*) (Table 2.6).

2.5 Discussion and Conclusions

Temperature had a significant effect on growth performance of juvenile northern cod during and following stock collapse. The year classes born in the late 1980s and early 1990s experienced very cold ocean conditions in their early years and were slower growing than year-classes born later in warmer conditions.

The positive impact of temperature on the growth of juvenile cod was cumulative in age 1-4 fish examined here. Brander (1995) used weight as a growth metric to suggest that 92% of observed variability among stocks in size-at-age for 2-4 year old fish could be explained as a linear function of temperature. Brander (1994) also reported a 29% increase in size-at-age per 1 °C temperature increase over the range of cod stocks. The increasing strength of the effect of temperature after the first two years of life could also relate to stage-specific energy allocation differences. For example, it is known that youngest northern cod are more tolerant of cold water than are adults (Anderson and Rose, 2001), with high levels of blood antifreeze representing an apparent adaptation for survival in sub-zero ambient temperatures (Kao and Fletcher, 1988; Goddard et al., 1992). This antifreeze protection is reduced with age, thus it could be that youngest juveniles divert more energy toward this process than older fish, at the expense of other life processes such as growth.

Our findings suggest that the poor growth performance and associated productivity loss in juvenile northern cod during stock collapse was largely an environmentally-driven occurrence. Production rates in fish stocks reflect the total elaboration of new body substance in a unit of time (Ricker, 1975). Productivity gains are realized when inputs from reproduction, growth, and ultimately recruitment, exceed losses from natural or fisheries-induced mortality. Top-down forcing factors from fishing mostly adult cod have been ascribed as influencing productivity declines associated with stock collapse via intrinsic population responses such as depensation or Allee effects (Shelton and Healey, 1999; Frank and Brickman, 2000; Rowe and Hutchings, 2003) and rapid genetic selection toward small and early maturing fish (Olsen et al., 2004; Hutchings, 2005). For northern cod juveniles, however, productivity declines are unlikely to be explained by any of these factors as they were not fished, and poor growth appears to have been a function of cold sea temperatures. Moreover, once conditions improved, juvenile growth increased.

Previous studies have suggested that cold conditions that occurred throughout Atlantic Canada in the mid-1980s (DFO, 2014) were associated with declines in productivity of cod stocks throughout the region beginning circa 1985 (Rothschild, 2007; Hilborn and Litzinger, 2009). Our results suggest that cumulative impacts from this cold period could have been affecting northern cod juveniles prior to our ability to track year classes beginning in 1989 and influenced stock collapse. For example, there was a substantial decline in the abundance of age 2 and 3 cod captured in annual offshore trawl surveys in the mid-1980s (Brattey et al., 2008), concomitant with the cold period. Moreover, a similarly cold event occurred in the early to mid-

1970s (DFO, 2014), which could have plausibly affected stock productivity in a similar way. It is not unreasonable to speculate that the productivity of this stock had been overall declining for decades prior to stock collapse due to cumulative and resonating effects of cold events prior to the early 1990s.

Although temperature appears to exert some direct effect on growth, it also acts indirectly in cod and other fishes in affecting energy allocated to physiological life processes (Jobling, 1988; Sundby, 2000; Morgan et al., 2010). Energy use in organisms is partitioned among three broad categories of survival, growth, and reproduction, with allocation trade-offs influencing life history attributes and physiological performance. The indirect impacts of temperature are complex. For example, the prey species available to cod is affected by temperature, and the type of food available resonates to affect energy budgets (Rideout and Rose, 2006). Even if temperatures are favourable, growth may not be optimal if food is of poor quality or limiting (Brett, 1979; Anderson and Dalley, 2000; Mello and Rose, 2005). A recent laboratory study of age 4-5 northern cod showed that fish in poor condition regained growth and condition very quickly when subjected to favourable feeding conditions (Mullowney and Rose, 2013), thus we cannot conclude that the effect of temperature on growth rates of juvenile cod in the present study was fully direct, as synergistic effects with the forage base are probable.

The data did not allow us to determine growth trends for year classes born before the stock collapse, from 1992-1995, or for fish born after 2001. It is difficult to directly compare sizes of fish from other published studies on inshore juvenile northern cod because all used standard (SL – to end of caudal peduncle) and not total length. Brown et al. (1989) suggested that growth

rates at Bellevue, as interpreted from modal progression of age 0 fish, decreased from July 1982 to August 1983 as temperatures in the annual cycle decreased. For example, the primary mode remained at about 7.5 cm SL from January to March (calendar days 7 to 98). Methven and Schneider (1998) reported distinct modes at about 6-7.5 cm and 12-14 cm SL in trawl and seine size frequency distributions from collections at several sites in Trinity Bay from July-December 1991. Although the fish were not aged, the 12-14 cm mode likely reflects one year olds, which were only slightly smaller than our observed average of 14.3 cm total length across the four squid trap sites in that year. Overall, the SLs reported from these studies are consistent with the present total length data, and reinforce the conclusion that growth declines occurred in juvenile year classes during the period of collapse in the early 1990s. Moreover, they suggest only minor spatial differences in growth rate in cod juveniles along the northeast coast of Newfoundland.

In offshore areas of the northeast coast, cod aged 2-4 captured in survey trawls in the Northwest Atlantic Fisheries Organization Divisions 2J, 3K, and 3L during the autumns of 1992-1998 showed either stability or slight increases in size (Lilly, 1997; Brattey et al., 2010). Also, in the period following this study, Renkawitz et al. (2011) showed age 1 juveniles captured in beach seines in Newman Sound, Bonavista Bay, grew from about 6 cm SL in May-June to about 11 cm SL in September in 2002 and from about 8 cm SL in May-June to about 13 cm SL by September in 2003. Again, given differences in sampling times and measurement methodologies, these estimates seem similar to the average sizes of 11.2 and 13.2 cm total length reported for one year olds from Smith Sound in the winters of 2000 and 2001. Further, the improvements seen from 2002 to 2003 imply the increasing trend in growth rates reported

from 1998-2001 continued in subsequent years. The present data, in conjunction with the available literature, are depicting a broad-scale scenario of gradual improvements in juvenile cod growth concomitant with warming of the Newfoundland and Labrador shelf since the mid-to-late 1990s.

There are several potential biases that could influence results. The spatial inconsistencies among surveys conducted in the two periods, the cold early 1990s and the warming late 1990s and early 2000s, could produce bias. It would appear minor however as there was little evidence of spatial variation in growth rates among the present study sites, and the initial Bellevue site was in close proximity to Smith Sound, the focus of the latter period surveys. Moreover, Methven and Schneider (1998) reported similar growth in juveniles in 1991 at other survey locations in Trinity Bay. Notwithstanding spatial inconsistencies of the surveys, timing differential across the two surveys could also be an issue. With the Smith Sound trawl surveys conducted in January, roughly 5-8 months ahead of the squid traps surveys, differences in absolute sizes of fish across the two surveys, with Smith Sound fish captured in the post-collapse period being bigger, would likely be conservative estimates. This bias however would not likely have much impact on growth rate analyses and conclusions. Further, bias could have been introduced from differing spawning times among sites and years in relation to survey timing, but size-at-age was most consistent in the first two years of life with increasing divergence thereafter, which suggests that spawning timing among sites did not differ greatly within years. Finally, differences in gear catchability between the squid traps and Campelen trawl could have introduced unknown bias in the size distributions of samples.

In conclusion, the weight of evidence indicates that decreasing temperature exerted a strong negative effect on growth performance and associated productivity in northern cod juveniles during the stock collapse in the early 1990s, and that increasing temperatures in the late 1990s and 2000s have subsequently enabled improvements in growth. These impacts appear to have been spatially broad-based with little difference in growth rates of year classes across inshore sites. Temperature impacts strengthen with age and cumulative temperature is a strong driver of growth rates in juvenile northern cod. Overall, warm conditions promote superior growth and improved productivity in this stock and if warming persists recent productivity improvements (DFO, 2014; Rose and Rowe, 2015) would be expected to continue.

2.6 Acknowledgements

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2.8 Figures

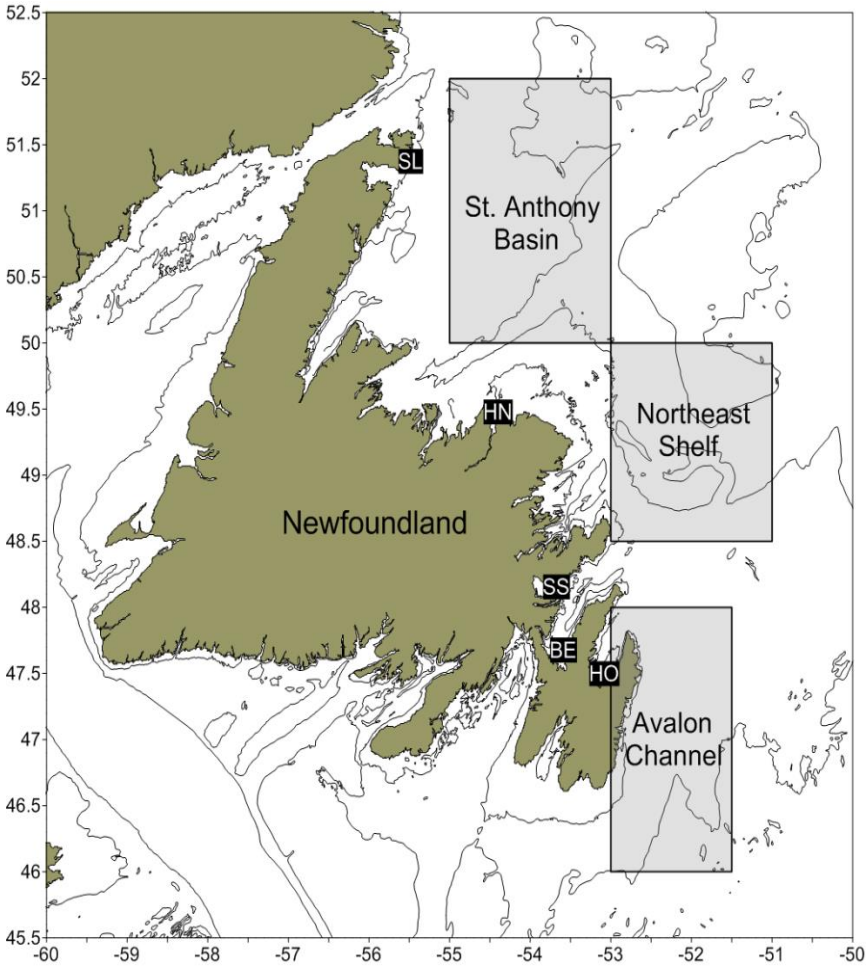

Figure 2.1. Map of Newfoundland and Labrador (brown) and 100m and 300m depth contours of the continental shelf (grey underlay). Locations of place names contained in the analysis: Squid trap locations – St. Lunaire (SL), Herring Neck (HN), Bellevue (BE), and Holyrood (HO). Trawl survey location – Smith Sound (SS). Petrie Boxes shaded in grey.

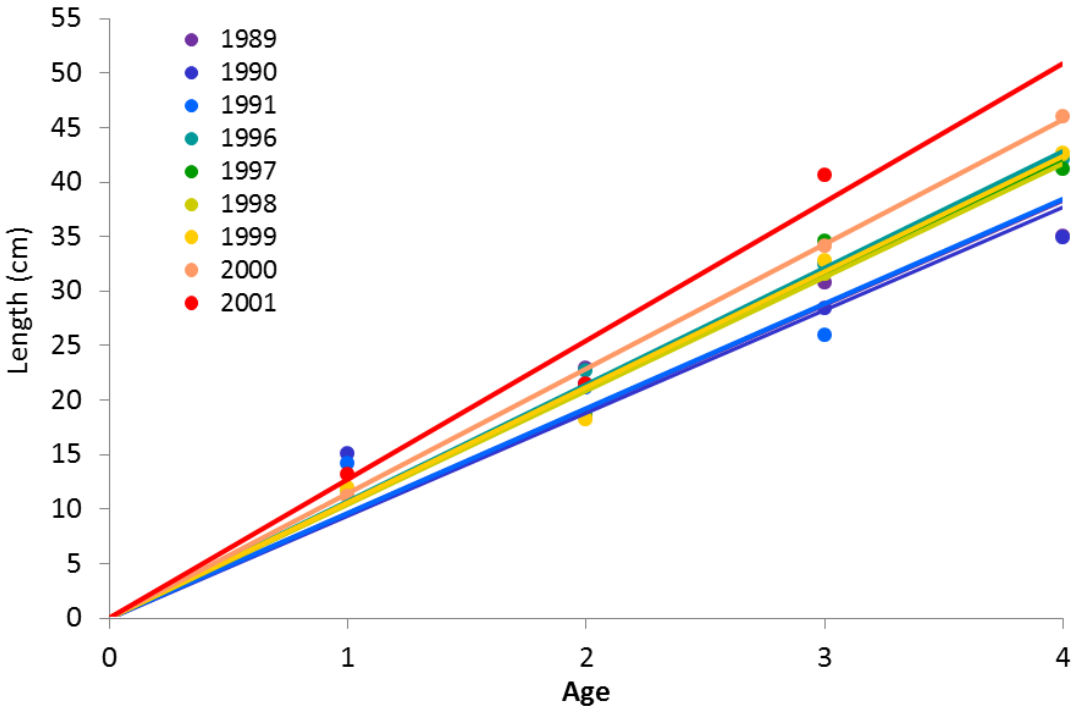

Figure 2.2. Annual mean lengths-at-age and associated linear regression growth curves for year classes captured in squid trap and bottom trawl surveys.

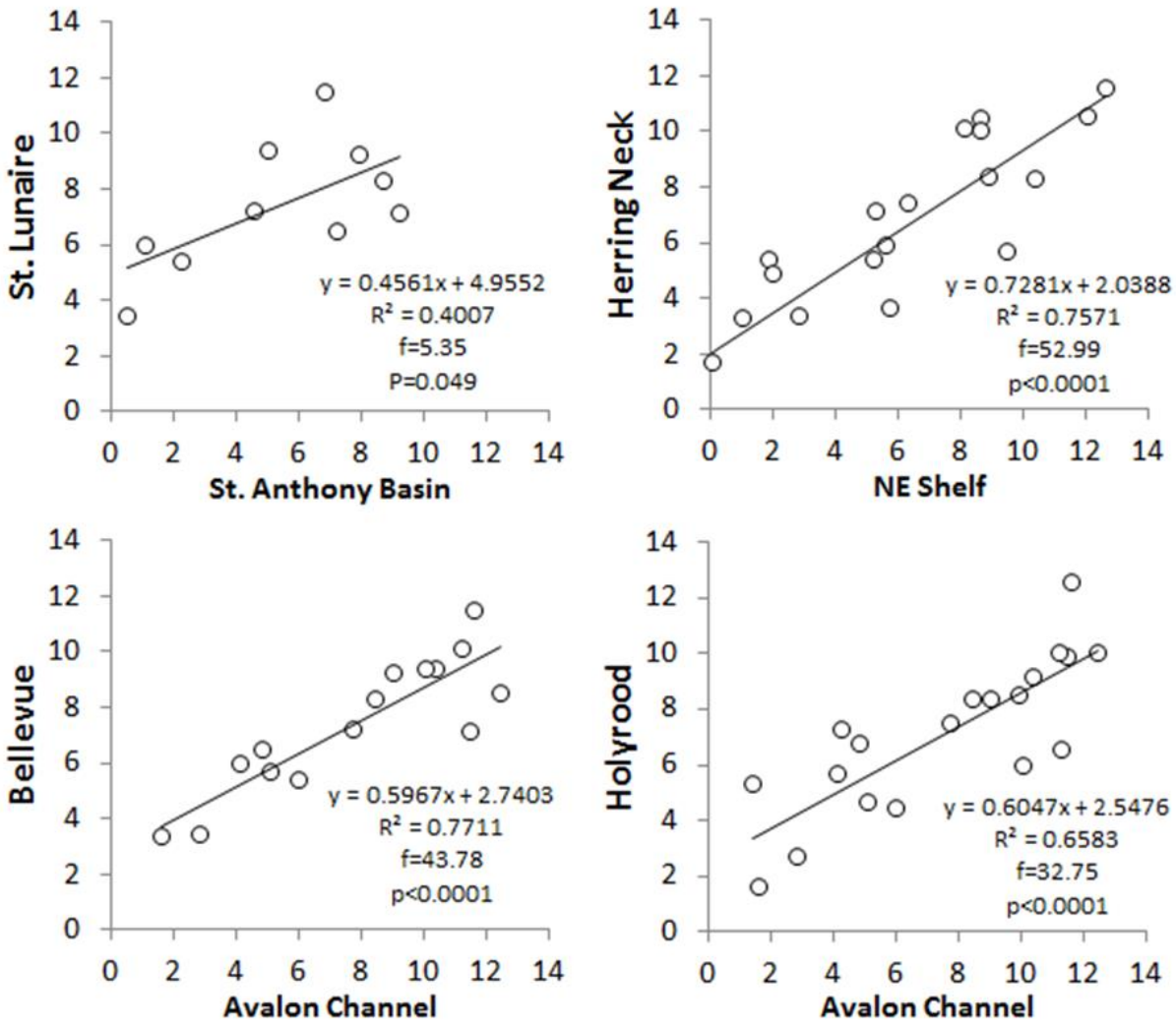

Figure 2.3. Relationships between monthly sea surface temperatures in offshore Petrie Boxes versus thermographs from inshore squid trap surveys. Individual points denote monthly averages when both sources of data were present from 1991-1994.

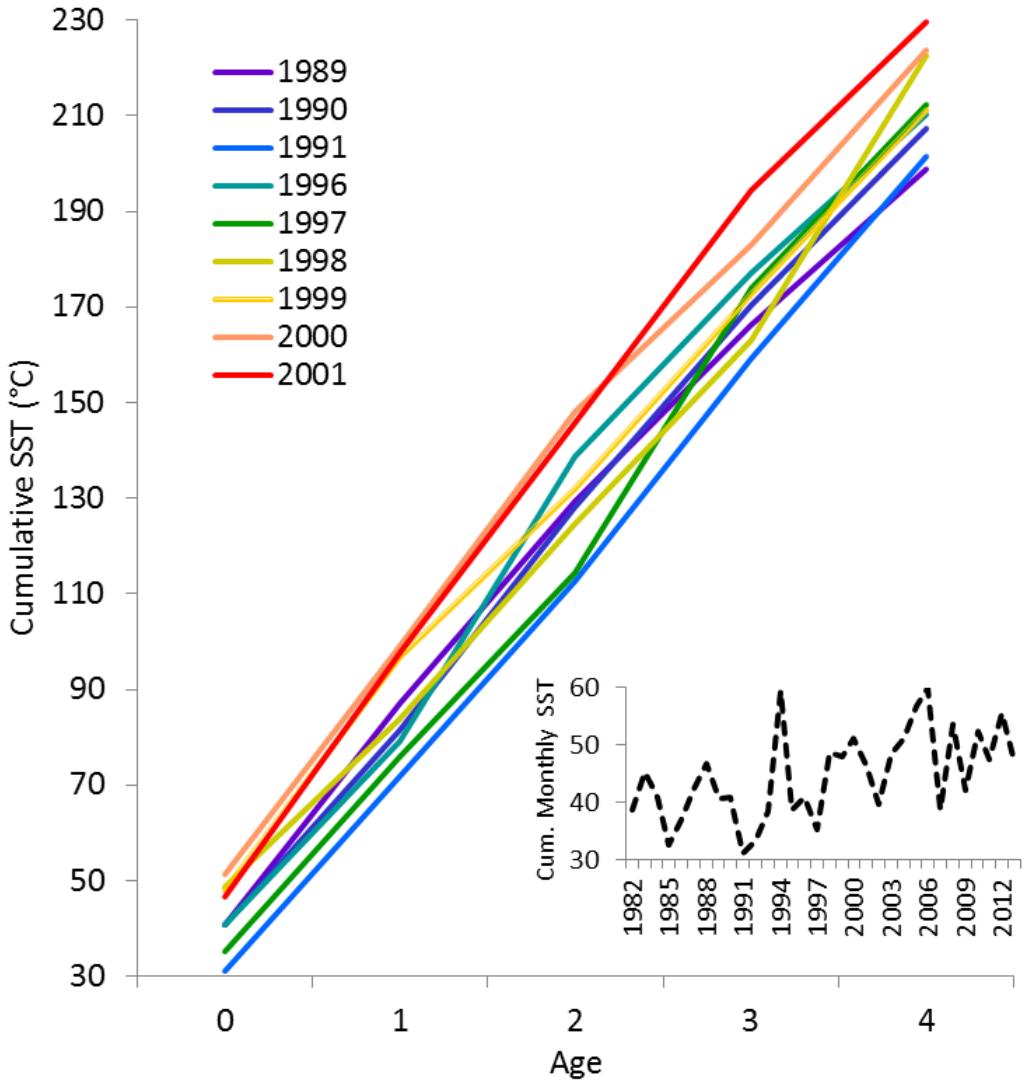

Figure 2.4. Cumulative sum of monthly sea surface temperatures by year (dashed black line in inset) and cumulative sums of monthly sea surface temperatures-at-age experienced for each year class.

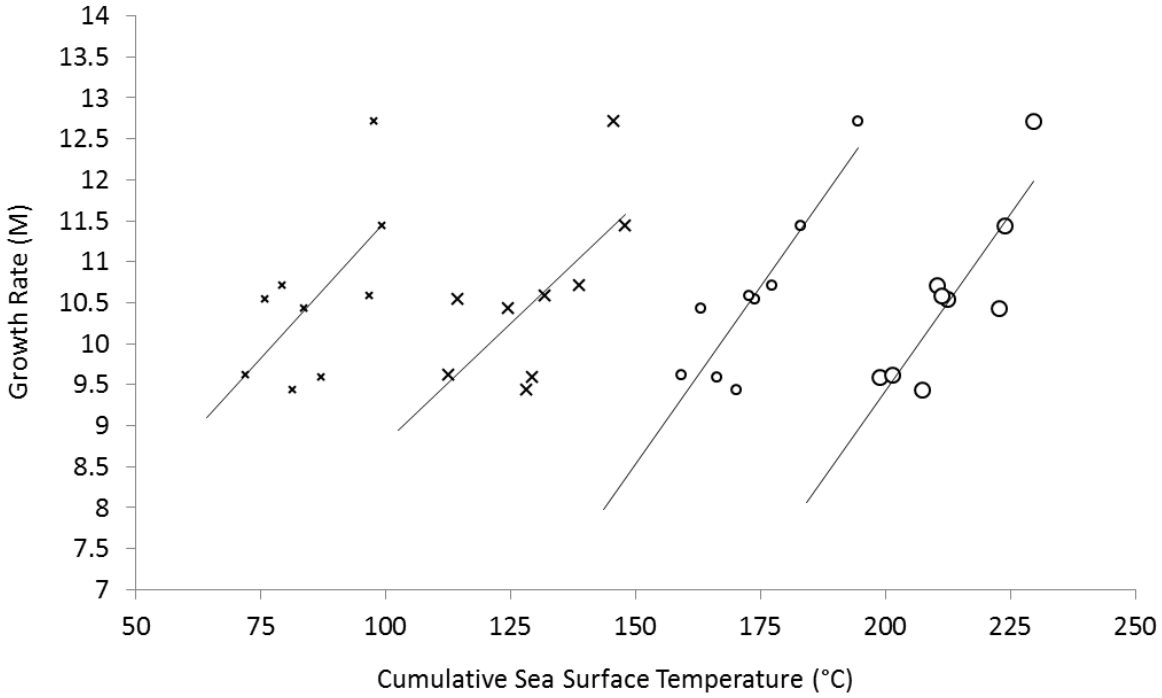

Figure 2.5. Age-specific distributions of growth rates versus cumulative sea surface temperatures experienced throughout life for juvenile cod captured in squid trap and bottom trawl surveys. Individual points represent year classes at any given age. Age 1=x, age 2=X, age 3=o, age 4=O.

2.9 Tables

Table 2.1. Squid trap sample sizes of number of cod captured by age, location, year, and month.

	Year	1991				1992				1993				1994			
	Age	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
St. Lunaire	May																
	June									2	43	69	14				
	July						24	62	10	2	53	105	31				
	Aug.					6	48	67	6	7	66	42	3				
	Sept.					17	45	42	6	20	92	26	2				
	Oct.					35	71	17	3	38	49	11	1				
	Nov.					4	1			4							
	Dec.																
Herring Neck	May						2	2		2	28	29	5		17	34	50
	June					9	66	36	7	12	71	55	11	3	13	73	100
	July					4	33	26	3	8	29	41	21	97	27	37	27
	Aug.					4	75	46	4	13	38	51	11	61	15		
	Sept.						43	45	3	20	75	104	4	1	15	8	5
	Oct.					1	22	23	3		2	4	1			1	
	Nov.						1	6		1	3	3			2		
	Dec.																
Bellevue	May					18	20	11	1	3	44	27	5				
	June					16	75	23		19	73	62	5				
	July					12	60	17		10	79	57					
	Aug.					20	66	40	1	13	69	35	2				
	Sept.	631	323	62	5	44	57	11	2	17	79	28					
	Oct.	536	366	19	2	31	24	11	4	37	47	49	4				
	Nov.	193	103	23	25	5	20	12	1	14	10	4					
	Dec.	38	5		1												
Holyrood	May					12	16	12	4	11	21	14	1	6	37	3	
	June					26	63	12		18	63	64	1	22	48	29	3
	July					25	67	13		19	56	39		18	68	69	20
	Aug.	7	692	102	5	29	38			28	77	27		40	53	35	1
	Sept.	125	32	35	1	14	7			20	147	48	1	60	8	7	
	Oct.	156	46	1	1	8	38	8		51	32	23	3	40	18	13	1
	Nov.	13	55	6		3	24	13	1	8	3		8		7	1	
	Dec.		6	2													

Table 2.2. Smith Sound trawl sample sizes of number of cod captured by age and year. All surveys were conducted in mid-January.

	Year						
Age	1998	1999	2000	2001	2002	2003	2004
1		3	2	5	5		
2	6	22	10	19	0	2	
3	15	17	153	38	18	20	5
4	13	144	366	93	68	152	187

Table 2.3. General linear model on factors affecting length in juvenile cod captured in squid trap surveys. Main and second-order interaction effects shown.

Source	DF	Type IV SS	Mean Square	F Value	Pr > F
age	3	0.36833572	0.12277857	70.9	0.0002
locale	3	0.00292893	0.00097631	0.56	0.6621
year class	6	0.07610101	0.0126835	7.32	0.0226
age*locale	9	0.02984182	0.00331576	1.91	0.2456
age*year class	6	0.01785382	0.00297564	1.72	0.2845
locale*year class	14	0.02276046	0.00162575	0.94	0.58

Table 2.4. Data on fish lengths, growth rates, and ambient temperature-at-age. M denotes slopes of linear regression growth curves, r^2 are correlation coefficients of model fits, observed values are mean length-at-age, predicted values are from linear regression growth models for each year class, residuals calculated as observed-predicted values, and CumTemp is cumulative temperature-at-age calculated from monthly sea surface values at Petrie Box locations.

Year Class	M	r^2	AGE	Observed	Predicted	Residual	CumTemp
1989	9.59	0.60	1		9.59		87.22
			2	22.96	19.19	3.77	129.40
			3	30.80	28.78	2.01	166.40
			4	34.99	38.38	-3.39	198.82
1990	9.43	0.79	1	15.10	9.43	5.67	81.54
			2	21.43	18.86	2.56	128.11
			3	28.38	28.29	0.09	170.29
			4	34.96	37.72	-2.77	207.29
1991	9.61	0.52	1	14.23	9.61	4.62	71.93
			2	21.18	19.21	1.97	112.58
			3	25.97	28.82	-2.85	159.15
			4		38.43		201.34
1996	10.71	0.99	1		10.71		79.31
			2	22.67	21.43	1.24	138.82
			3	32.41	32.14	0.27	177.23
			4	42.03	42.85	-0.82	210.39
1997	10.54	0.94	1		10.54		75.86
			2	18.55	21.07	-2.53	114.41
			3	34.59	31.61	2.98	173.92
			4	41.17	42.15	-0.98	212.33
1998	10.43	0.98	1	11.67	10.43	1.23	83.83
			2	18.30	20.87	-2.57	124.60
			3	31.58	31.30	0.28	163.14
			4	42.51	41.74	0.77	222.65
1999	10.58	0.98	1	12.00	10.58	1.42	96.74
			2	18.21	21.16	-2.95	131.84
			3	32.78	31.73	1.04	172.61
			4	42.64	42.31	0.33	211.15
2000	11.44	0.99	1	11.20	11.44	-0.24	99.22
			2		22.88		147.95
			3	34.10	34.32	-0.22	183.05
			4	45.99	45.76	0.23	223.82
2001	12.71	0.95	1	13.20	12.71	0.49	97.70
			2	21.50	25.43	-3.93	145.71
			3	40.60	38.14	2.46	194.44
			4		50.86		229.54

Table 2.5. Linear regression model equations, fits, and significance for relationships of growth rates with cumulative temperature-at-age.

Age	Symbol	equation	r^2	f	p
1	x	y = 0.0673x + 4.7802	0.42	5.11	0.058
2	X	y = 0.058x + 3.003	0.48	6.52	0.038
3	o	y = 0.0865x - 4.4378	0.80	28.58	0.001
4	O	y = 0.0864x - 7.8549	0.75	21.52	0.002

Table 2.6. General linear model on the effects of age and cumulative temperature-at-age in affecting lengths for cod year classes captured in squid trap and bottom trawl surveys. Main and interaction effects shown.

Source	DF	Type III SS	Mean Square	F Value	Pr > F
age	3	0.05989835	0.01996612	2.97	0.054
cumTemp	1	0.04711162	0.04711162	7.01	0.0147
cumTemp*age	3	0.12428985	0.04142995	6.16	0.0033

Chapter 3

Is recovery of northern cod limited by poor feeding: the capelin hypothesis revisited

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Chapter 3 examines growth and condition of post-collapse northern cod from an inshore location where growth and condition were similar to pre-collapse norms in relation to an offshore location where growth and condition were very poor. Complementary analyses are conducted on subjects held in tanks as well as in wild fish from both locations. The study finds that poor growth and condition in the offshore is related to a poor diet, deficient in capelin and laden with shrimp. Interestingly, in contrast to chapter 2, temperature differences did not account for differences in growth of these larger fish. However, the chapter complements chapter 2 in establishing that bottom-up processes were integral in regulating post-collapse northern cod and bridges the gap for an examination of factors affecting the ecosystems key conduit, capelin, following the period of stock collapses.

3.1 Abstract

The slow recovery of the 'northern' Atlantic cod (*Gadus morhua*) stock off Newfoundland and Labrador has been ascribed to many factors. One hypothesis is poor feeding and condition as a consequence of a decline in capelin (*Mallotus villosus*), their former main prey. Comparisons of the growth and condition of cod from known inshore (Smith Sound) and offshore (Bonavista Corridor) centres of rebuilding were made on wild versus captive subjects fed an unlimited diet of oily rich fish. Wild fish in these areas have had different diets and population performance trends since stock declines in the early 1990s. Captive cod from both areas grew at the same rates and achieved equivalent prime condition, while their wild counterparts differed, with smaller sizes, lower condition in small fish, and elevated mortality levels in the offshore. Environmental temperature conditions did not account for the differences in performance of wild fish. The results suggest that fish growth and condition, and hence rebuilding in the formerly large offshore spawning components of the northern cod, have been limited by a lack of capelin in their diet. It is suggested that these groups are unlikely to rebuild until a recovery in capelin occurs.

3.2 Introduction

The collapse of the 'northern' Atlantic cod (*Gadus morhua*) stock complex off Newfoundland and Labrador during the late 1980s and early 1990s and subsequent slow recovery are well known (Rose, 2007, Lilly, 2008). Phenomena associated with the belaboured recovery have included high natural mortality rates (Rose and O'Driscoll, 2002; Lilly, 2008), early maturation (Fudge and Rose, 2008), reduced growth (Shelton et al., 2006), and poor condition (Sherwood et al., 2007). Since the collapse, the remaining fish in the formerly dominant offshore groups of this widespread stock complex have had a contracted life history, with few fish surviving beyond about age 6 (Brattey et al., 2010), whereas historically maturation did not occur until ages 6-7. From the early 1990s, and over the following decade, the remnant groups of extant offshore northern cod were comprised of relatively young fish in poor condition, especially in spring when condition is most critical (Mello and Rose, 2005a). Only in the past few years has there been evidence of older fish in good condition (G.A. Rose, unpublished data).

The northern cod complex includes both coastal and offshore spawning groups (Lilly, 2008). Coastal areas were fished historically for hundreds of years (Rose, 2007), almost certainly on both coastal and migratory offshore groups, but all areas were fished heavily from the 1960s until the closure of the fisheries in 1992. Fishing mortality in the coastal areas likely exceeded that of the adjacent offshore, at least during the later period (Myers et al., 1997). Nevertheless, in 1995, with overall stock abundance at its lowest point, a large spawning aggregation formed in Smith Sound, Trinity Bay (Figure 3.1), where there was little historical evidence of large

groups of cod (Rose et al., 2011). The founder year-classes of the Smith Sound group were born in 1989 and 1990, and it grew from about 10,000 t in 1995 to 26,000 t by 2000 (Rose et al., 2011). In contrast to their offshore counterparts, these inshore fish commonly survived to advanced ages (i.e. 8-15 years) throughout the 1990s and early 2000s and maintained mortality, weight- and length-at-age profiles that closely reflected pre-collapse northern cod (Rose, 2004; 2007; Rose et al. 2011). Only small genetic differences have been reported for fish collected from the Bonavista Corridor (offshore – Figure 3.1) and Smith Sound (Ruzzante et al., 1999; Rose et al. 2011), consistent with the two groups comprising components of a meta-population (Smedbol and Wroblewski, 2002). While important phenotypic differences can occur in cod groups with close genetic association (Marcil et al., 2006 a;b), genetic similarity of these two groups suggests that differing life history and other closely associated attributes are largely environmentally driven effects on plastic phenotypic traits.

An often overlooked part of the many descriptions of the collapse of the northern cod is that its chief food, the capelin (*Mallotus villosus*), declined abruptly at about the same time (Carscadden et al., 1997; DFO, 2011). Capelin abundance has remained very low since, and a lack of capelin has been suggested as a bottleneck to the regaining of condition and rebuilding of the northern cod (Rose and O'Driscoll, 2002). Recent diet studies have confirmed the reduction in capelin in the cod diet that followed the precipitous declines of these species (Dawe et al., 2012; Krumsick and Rose, 2012). Pandalid shrimps, which are poor in essential lipids compared to other species of the forage domain (Lawson et al., 1998), became the chief food of offshore northern cod in the 1990s, comprising as much as >95% of the diet in some

areas (Sherwood et al., 2007; Krumsick and Rose, 2012). It has remained untested, however, whether the life history changes in the offshore component of the stock would be ameliorated if cod had access to their historical diet, in particular to an abundance of capelin.

The primary objective of this study was to determine if the documented changes in wild offshore cod, including reduced growth, poor condition, elevated fecundity, and increased mortality would be maintained if fish were fed capelin and other fishes rich in lipids. The hypothesis was that growth, condition, and mortality rates would all improve in the presence of a lipid-rich diet. Direct comparisons of performance of these biological metrics between offshore-captured fish from the Bonavista Corridor (NAFO Subdivisions 3KL) to a control group of inshore-captured fish from Smith Sound (3L) during a two-year monitoring project in which both groups were fed a diet rich in oily fish (primarily capelin) were made. Further comparisons between these fish reared under controlled conditions to those occurring in their wild counterparts were conducted. An examination of the energy content of potential prey species of northern cod was done to determine their potential influence on growth and condition in pre- and post-collapse periods. Finally, the role that temperature might play in regulating northern cod population dynamics was investigated.

3.3 Methods

3.3.1 Trends in Wild Fish

In both Smith Sound and the Bonavista Corridor (Figure 3.1), wild fish were captured in research sets made on cod aggregations during the winter and spring from 2002-2006, spanning the time the experimental cohorts were at liberty. All fish were sampled for total lengths and total weights. In addition, a macroscopic analysis of stomach contents was conducted (see Sherwood et al. 2007 for details) and otoliths were collected for subsequent aging. All sampling was done under permits from the Department of Fisheries and Oceans Canada (DFO).

Age frequency distributions were plotted to interpret demographic and structural differences between groups. Group-specific total mortality rates (Z) were estimated as the exponential rates of decline for fully selected ages (4-10 years), analogous to the catch curve method. Age-specific condition indices were determined using Fulton's condition factor ($k = 100\ W/L^3$) (Lambert and Dutil, 1997) for mean lengths and weights in each group, limiting the analysis to age 2-6 fish due to insufficient sample sizes at younger and older ages, particularly in the Bonavista Corridor group. Finally, group-specific lengths- and weights-at-age were plotted and compared. Statistical differences for each of these biological metrics (abundance, mortality, condition, length, weight) were tested using general linear models (GLMs), regressing the dependent variable(s) against the main and interaction effects of group and age.

3.3.2 Trends in Captive Fish

Offshore cod from the Bonavista Corridor (Figure 3.1) were captured with a Campelen research trawl from the CCGS *Teleost* on March 13, 2007 from depths of about 350 m. These fish were brought live to the Ocean Sciences Centre (OSC) of Memorial University of Newfoundland,

where experimentation took place under a protocol approved by the Animal Care Committee of the University. Approximately 50 fish survived the initial capture and transport and were housed at the OSC in a 23,500 L tank. Fish were in poor condition when captured (the condition of these fish was not measured at time of capture or during early stages of captivity in an attempt to minimize stress, but measures from their counterparts at sea are given in Figure 3.2). Initial mortality was high, with only 12 fish surviving and in good condition by Apr. 12, 2007 (Table 3.1). These fish were fed *ad libitum* with capelin, squid (*Illex argentinus*), herring (*Clupea harengus*), and mackerel (*Scomber scombrus*). The bulk of the feed was capelin.

The capture of inshore Smith Sound fish from Trinity Bay (Figure 3.1) was intentionally delayed to allow the Bonavista Corridor fish to be stabilized and show no adverse signs of their capture before beginning experimentation. In mid-September, 2007, 34 fish approximating the lengths of the surviving Bonavista Corridor fish were captured in cod pots in <50 m of water in Smith Sound (Table 3.1). These fish were transported to the OSC and placed in an adjacent tank identical to that of their offshore counterparts, with the same water supply. The Smith Sound fish were initially in superior condition to that of the Bonavista Corridor fish and acclimated quickly to the tank. They began feeding almost immediately, with only a single mortality within the first few days of being housed, and were stabilized and ready for experimentation soon after arrival. Statistical testing for differences in initial population structure across groups by length and age were conducted using a GLM.

Tank temperatures were maintained close to natural ambient near surface temperatures, with water pumped from the adjacent sea. Temperature cycled seasonally from about 11.5-12°C

during late summer and early fall to 2-4°C during late winter and early spring. When temperatures exceeded 10°C cooling was applied using a chiller system. Dissolved oxygen was kept constant at about 95-100% during all phases of the project. Water volumes in the tanks were kept at levels to approximate equal densities of fish in the two experimental groups.

After each group had acclimated to the tanks and prior to beginning the experiment all fish were implanted with passive integrated transponder (PIT) tags in the abdomen so performance could be individually tracked. A mild dose of MS222 was given to each individual prior to surgery and each fish was monitored for 2 hours afterwards. A regular regiment of environmental monitoring and measurements was conducted throughout the period of captivity. This included daily measures of water temperature and chemistry. On a quasi-monthly schedule, individual fish were removed from each tank, sedated with a minimal dose of MS222, then measured for length and weight and examined for external evidence of reproductive output. No fish died during or subsequent to being measured or PIT tagged.

Experimental feedings of the Bonavista Corridor fish began on Aug. 10, 2007, and the Smith Sound fish on Sept. 28, 2007. The experiment ended in January, 2009. In total, experimental feedings of the Bonavista Corridor fish lasted for 550 days and for Smith Sound fish 472 days. During this period, both groups were fed twice weekly *ad libitum* measures of the pre-experimental diet supplemented with shrimp (*Pandalus borealis*) and additional capelin. The volume of the diet was not strictly controlled; rather, it was delivered to feed fish to satiation. Prey type varied during the experiment, but each day-specific offering was of identical composition in the two tanks.

Beginning in March, 2008, egg collectors were placed in both tanks, with the spawning period occurring from about April 26 – July 15, 2008. During this time eggs were continuously removed from the surface of each tank. Volumes of both dead and living eggs were estimated and living eggs were kept and raised to the fry stage, which confirmed viability. The ages, sexes, and maturities of individuals were determined through autopsy upon death during the experiment or when all fish were sacrificed by overdose with MS222 at the termination of the study. Maturities were based on gonad development (Morrison, 1990), with ages determined by otolith interpretation.

The initial experimental groups were examined by size, age, and sex to investigate potential demographic differences. Age 3 fish were removed from all analyses pertaining to growth, mortality, and condition because their poor growth and early mortality in both experimental groups suggested competitive exclusion from food within each tank.

Age-specific growth rates by both length and weight were plotted and modeled to investigate if statistical differences existed between the two groups. For both growth metrics, GLMs were used to examine growth rate differences by area of origin, age, and sex over time, regressing the continuous covariate day against the three class variables and examining interaction effects. The dependent variable constituting growth rate in the models was calculated as the length (or weight) of an individual on any given sampling day minus the length (or weight) of that individual on the previous sampling day. Models were conducted on the raw growth rate data but observations from day 550 were removed from the weight analysis because they were an outlier (i.e. 2.8 s.d. from mean [higher]).

Cod condition was determined from individual weight and length measurements using a modified Fulton's condition factor (*k*), with whole weight used in lieu of somatic weight (total weight less gonad and stomach weight) because only whole weights were available from sampling of live individuals. Trends in age- and sex-specific condition over time for each group were plotted to qualitatively relate intraspecific condition throughout the experiment and statistical testing for differences by group, sex, age, and day were conducted using GLMs.

An index of cumulative volume of viable eggs per total length of spawning females (ml eggs/cm spawning females) in each tank was developed and used to relate the relative rates of reproductive output from the two groups. The index was additive for lengths of females in each tank, thus was based on the entire population and not individual fish in each tank.

Natural mortality was monitored throughout the experiment for age 4 and 5 fish within each group and a generalized linear model with a logit link function was used to examine mortality rates by day, area of origin, age, and sex. This analysis was limited to days 0-403 because a late-experiment water delivery accident in the Bonavista Corridor tank (day 465) led to three deaths that were unrelated to the experiment.

3.3.3 Environmental Conditions - Temperature and Diet

A spatiotemporal examination of bottom temperature in Smith Sound and the Bonavista Corridor was conducted to determine how ocean climate may have influenced population dynamics for both groups in the wild. Data utilized were a compilation from all surveys contained in DFO oceanographic databases, embedding data from programs such as the Atlantic Zonal Monitoring Program (AZMP), annual offshore trawl surveys, foreign research

surveys, and university research. Polygons capturing the entire area of Smith Sound and a 2400 nm² region around Bonavista Corridor were examined for trends in depth-specific temperature, limiting the analysis to the fall and winter periods (Sept. – Feb.) when data were most complete. Trends in mean temperatures of 50 m depth bins were examined to determine spatial thermal distribution. Data prior to 1980 were inadequate for analysis and omitted, and the available time series for Smith Sound was shorter, beginning in 1995, which reflects dedicated research interests in the Sound following the overwintering cod discovery in the mid-1990s. Annual temperatures for the two most frequently sampled bins in both areas (300-350 m for Bonavista Corridor and 150-200 m for Smith Sound) were plotted to examine and assess the potential influence of the long-term ocean climate in each area.

The diet of each wild group was qualitatively assessed from samples collected during 2002-2007 in each area (Section 3.1) using a mean partial fullness index (PFI) (Lilly, 1984), calculated as:

$$\mathrm{PFI}_i = \frac{1}{n} \times \sum_j^n \frac{w_{ij}}{L_j^{\,3}} \times 10^4$$

where w_{ij} is the weight of prey *i* for fish *j* (g), L_j is the length of fish *j* (cm), and *n* is the total number of stomachs sampled. This index, which relates the weight of each prey item in the stomach to the length of the predator, is robust in that it is not strongly influenced by frequent occurrences of small prey or infrequent occurrences of large prey. Prey items were categorized to the lowest possible taxonomic level, normally macroscopically, but by a dissecting

microscope if necessary. In most cases prey were identified to species, but grouped to higher taxonomic levels when necessary.

A Carbon Hydrogen Nitrogen (CHN) proximate composition analysis was conducted on three prey items common in the diet of northern cod: capelin, northern shrimp, and snow crab (*Chionoecetes opilio*). All samples were obtained from the eastern slope edge of the Grand Bank, approximately 200 nm southeast of Newfoundland (Figure 3.1), during early November, 2012. Individual whole animals of each species (Suppl. Table 3.4.) were initially frozen before being dried in a muffle oven at 55°C for 35 days, ground up using a commercial blender and morter and pestle, and subsequently dried for another week. Six replicates of each species were blasted in an *Exeter CE-440 Elemental Analyzer* with CHN compositions transformed into protein and lipid estimates following the conversion methods of Gnaiger and Bitterlich (1984). Energy density was calculated using published estimates for lipid (39.3 kJ/g) and protein (17.8 kJ/g) (Schmidt-Nielsen, 1997, Robards et al., 1999). Two controls, fish food of known CHN composition made by *Skretting* were tested to assess the accuracy of the results. The first was a coarse pellet used in cod aquaculture while the second was a fine pellet used in salmonid aquaculture. The coarse pellet composition of 54% protein and 22% lipid (versus nominal concentrations 50% and 18%) and fine pellet composition of 58% protein and 36% lipid (versus 47% and 28%) provided confidence in the CHN method.

3.4 Results

3.4.1 Trends in Wild Fish

A total of 3,139 cod were sampled from the offshore and 4,600 from the inshore. Smith Sound fish achieved greater ages (Figure 3.2a), with a mean age of 6.4 years contrasting with 3.8 years for Bonavista Corridor fish, a highly significant difference (Suppl. Table 3.5, $F_{1,7737}$=3131, p<0.01). Group-specific mortality rates in age 4-10 fish were significantly different (Suppl. Table 3.5, $F_{2,11}$=14.81, p<0.01), being much higher in the Bonavista Corridor (Z=1.25 yr^{-1}) than in Smith Sound (Z=0.17 yr^{-1}) (Figure 3.2b). Youngest (Age 2-3) Bonavista Corridor cod were in poorer condition than their Smith Sound counterparts (Figure 3.2c), but there was a high level of variability and no significant differences across the two groups as a whole (Suppl. Table 3.5, $F_{2,5631}$=16.97, p<0.01). Despite no differences in condition for most fish, Bonavista Corridor cod were consistently shorter (Suppl. Table 3.5, $F_{2,5632}$=12672, p<0.01) and lighter (Suppl. Table 3.5, $F_{2,5636}$=8195, p<0.01) than their Smith Sound counterparts (Figure 3.2d), although the differences disappeared at age 6.

3.4.2 Trends in Captive Fish

Cod collected from the inshore and offshore sites were well matched in size (Figure 3.3a) and age composition (Figure 3.3b) at the beginning of the experiment (Suppl. Table 3.6), although sample sizes differed (Bonavista Corridor n=12, Smith Sound n=33). Offshore and inshore fish averaged 48 cm and 49 cm respectively and both groups had a mean age of 4 years. Consistent

with the disparity in sample sizes, there were greater numbers of individuals at most sizes in the inshore group, especially in the 40-54 cm size range.

Age 4 and 5 fish in both groups grew in uniform fashion throughout the experiment while growth in age 3 fish from both groups was poor (Suppl. Table 3.7). There was consistency in the pattern of growth rates with both weight and length gain slowing down prior to and during the spawning period but increasing thereafter (Figure 3.4). Virtually all variability in growth rates was attributable to time (day), with no statistical differences in growth rates of age 4 or 5 fish both within and across groups by either metric (Table 3.1).

Bonavista Corridor females had a more prolonged period of high condition than all other fish. Condition of all fish fluctuated throughout the experiment (Suppl. Table 3.8) with a general pattern of peaking prior to spawning, declining through the spawning period, and increasing thereafter (Figure 3.5). Statistically, sex interacted significantly with both area (Table 3.2, $F_{1,344}$=18.78, p<0.01) and age (Table 3.2, $F_{1,344}$=19.10, p<0.01) to produce the pattern of a delay in condition decline in age 4 and 5 Bonavista Corridor females, which was most pronounced in age 5 fish.

The spawning period began on about day 260 in both groups (Figure 3.6). Initial relative egg output was near identical but a divergence occurred during the latter half of the spawning period with output increasing most substantially in the Bonavista Corridor group. At the end of the spawning period the 18.0 ml eggs/cm spawning female from Bonavista Corridor fish was 53% higher than the output of the Smith Sound group.

All mortality in age 4 and 5 fish occurred during spawning (Figure 3.7) and there was no difference in mortality rates between groups. The logistic regression model (Table 3.3) showed that time (day) was the most influential factor affecting mortality (X_1^2=15.22, p<0.01) with no significant effect of age, sex, or area of origin. This likely reflects the association of mortality with the spawning period.

In relation to wild trends, cod from both groups achieved overall larger sizes in captivity, with the differences being especially substantial for the Bonavista Corridor fish (Suppl. Table 3.9). Captive Smith Sound cod that were initially age 4, measured on day 332 at 5 years of age, were on average 4% longer and 65% heavier than their wild counterparts. In comparison, Bonavista Corridor cod of the same cohort were on average 27% longer and 157% heavier than their wild counterparts. Similarly, age 6 fish (initially age 5) in the Smith Sound tank were no longer and about 30% heavier than their wild counterparts, while for Bonavista Corridor fish these differences averaged about 20% and 135% for length and weight respectively. These results suggest environmental conditions in the wild were especially poor in the offshore.

3.4.3 Environmental Conditions - Temperature and Diet

Smith Sound is a colder and shallower area than the offshore (Figure 3.8). Bottom temperatures in the Sound decrease with depth up to 225 m in both seasons, with a slight increase in the deepest 275 m regions, while the shallow and surface waters show high seasonal variability. In contrast, the deeper and offshore Bonavista Corridor temperature gradient increases from shallow to deep areas, with shallowest (225 m) areas averaging about 2.2-2.5 °C and deepest areas (≥ 475 m) about 3.75-4.5 °C. The cold temperature conditions in Smith Sound have been

relatively consistent since 1995 while in the Bonavista Corridor temperatures were cooler during the 1980s and early 1990s than since.

Cod diet was more diversified inshore than offshore (Figure 3.9). The PFI analysis revealed that shrimp were the primary prey of offshore cod, with capelin making a secondary contribution and all other prey contributing marginally. In contrast, in the inshore, capelin were the primary food with a diversity of species such as crab, shrimp, gadoids, other fishes, zooplankton, and benthos making lower-level contributions. Interestingly however, despite containing a comparatively non-diverse diet, the offshore stomachs were generally fuller as indicated by an overall higher PFI. Proximate composition analysis (Suppl. Figure 3.10) revealed that capelin contained the highest proportion of lipids and had an energy density that was approximately double that of northern shrimp and one-third higher than snow crab.

3.5 Discussion

Could a poor diet be the critical mechanism limiting population productivity in northern cod, as hypothesized by Rose and O'Driscoll (2002)? The findings suggest so, as under favourable feeding conditions offshore northern cod were shown to be capable of achieving sizes, growth rates, and condition levels equal to that of their inshore counterparts and comparable to historical norms. This suggests that the small sizes and poor growth evident in offshore northern cod until recently have largely resulted from a suboptimal diet.

Poor performance in offshore wild northern cod has been manifest in several ways since the early 1990s. On a diet dominated by shrimp, these fish showed contracted age distributions,

small sizes, and high mortality rates relative to inshore cod whose diet was more diversified. Under experimental conditions, however, captive inshore and offshore fish showed no difference in growth and mortality rates when fed a fish-rich diet, providing direct evidence of diet as a limiting factor in their poor performance. Historically, northern cod relied heavily on capelin as prey (Rose and O'Driscoll, 2002), receiving about 50-60% of their annual energy budget from this species (Bundy et al., 2000). Consistent with the present results, recent studies have shown an abrupt switch from a capelin to shrimp dominated diet during the mid-1990s (Dawe et al., 2012; Krumsick and Rose, 2012) following the capelin decline (DFO, 2011).

In the adjacent northern Gulf of St. Lawrence, where a similar cod stock collapse occurred in the late 1980s and early 1990s, energy deficiencies were determined to be the primary factor affecting growth and survival (Lambert and Dutil 1997, 2000; Dutil and Lambert, 2000). In relation to inshore groups, offshore northern cod may be especially susceptible to diet deficiencies, requiring larger energy reserves to accommodate their migratory life history (Robichaud and Rose, 2004). Previous studies have shown that there are few adequate substitutes for capelin in the Newfoundland-Labrador (NL) shelf ecosystem and when capelin abundance is low the quantity of food consumed by cod decreases (Lilly, 1984, 1991). In contrast, our data indicated overall consumption was higher in the offshore where capelin was not the primary prey, with shrimp more common. Dawe et al. (2012) showed post-collapse northern cod stomachs from the offshore were dominated by shrimp and also suggested that northern cod may actively select against shrimp, relying on it only when superior prey are unavailable. In addition, the diet deficiency in offshore northern cod appears not to be a

function of overall prey abundance, but a lack of prey that provide adequate lipid for growth (and possibly reproduction, see Rose and O'Driscoll, 2002).

The dietary benefits of capelin over shrimp relate to differences in lipid content and energy density. Sherwood et al. (2007) showed that individuals consuming a predominately shrimp-based diet had low growth rates, poor condition, early maturation, and high mortality rates relative to those consuming a higher energy diet. The proximate composition analysis showed virtually no lipids in shrimp with capelin composed of about 45% lipid. However, these results should be treated with some caution as CHN analyses commonly produce highly variable results due to spatiotemporal and biological influences on specimens (MacCallum et al., 1969; Montevecchi and Piatt, 1984; Vollenweider et al., 2011), along with the methodological choice of elemental conversion factors (Gnaiger and Bitterlich, 1984; Vollenweider, 2000). Nevertheless, the results are similar to Lawson et al. (1998), who showed the percentage of lipids in capelin to be roughly four-fold that of northern shrimp with double the energy density. It follows that cod feeding largely on shrimp would have to consume much more of this prey by weight than capelin or other oily fish in order to accrue similar energy benefits. This deficit would likely be amplified by the higher energy costs associated with predation of more individual prey. The fuller stomachs yet lower condition of the offshore fish is consistent with both of these contentions.

Several sources of uncertainty exist in the study. First, replicates during the laboratory portion of the project were not feasible, hence any so-called "tank effect" cannot be ruled out. Second,

potential effects of unknown complications arising from past conditions and life experiences in wild subjects could not be assessed. Third, the two groups were captured with different gear types which could introduce unknown selectivity biases. Fourth, Bonavista Corridor fish were held longer in captivity, which could introduce unknown bias, either positively from longer exposure to a superior diet or negatively from longer captive effects. The prolonged stabilization period of the offshore Bonavista Corridor fish in the tank when the fish were being fed but no growth measurements were taken due to high mortality and poor condition could have exhibited some influence on subsequent measures of condition, egg production, and differences in physiological status from wild fish. Further, the surviving fish from the Bonavista Corridor could have represented a biased sample of the fittest fish, although at the beginning of the experiment they were in no better condition than those that had died. The assumption was that survivors were in the same condition as those that died but had not suffered fatal capture and transport damage that is common is fish trawled from >300 m depths and transported to land. Finally, small sample sizes were unavoidable, particularly from the offshore. Nevertheless, for frequently measured metrics such as length and weight this influence is likely to be minor, but for mortality the influence could be high.

It is noteworthy that diet appears to have a more important influence on growth and condition of large northern cod than temperature, as cod in colder Smith Sound had higher growth rates than those in the warmer Bonavista Corridor. Cold conditions are known to produce slow growth rates in various cod stocks (Ruzzante et al. 2000; Beacham et al., 2000; Purchase and Brown, 2000; 2001), but Morgan et al. (2010) found no effect of temperature on northern cod growth, with energy allocation to growth related more to factors such as prey availability.

Similarly, Mello and Rose (2005b) showed that when food was not limiting, cod growth increased in cold waters, but when food was limiting growth was reduced. This study showed that wild Smith Sound cod not only had a higher proportion of capelin in their diet, but a more diverse diet (see also Dawe et al., 2012), and concomitantly, better growth and lower mortality than their Bonavista Corridor counterparts. In keeping with this, it is asserted that in the southern ranges of Newfoundland cod, including the south coast (Mello and Rose, 2005b) and Smith Sound (Rose et al., 2011), cod were better positioned to endure the cooling environmental conditions of the late 1980s and early 1990s (Colbourne et al., 2012) because of a more diversified diet and greater availability of capelin (see Mello and Rose, 2005b). That these southern and inshore areas experienced relatively strong recruitment and growth in the late 1990s (Rose et al., 2008) while areas to the north were barren is thought not to be coincidence, but a direct outcome of more ample feeding conditions.

The Newfoundland and Labrador shelf has warmed since the mid-1990s, reaching record highs in 2010-2011 (Colbourne et al., 2012), which should benefit cod stocks via increased recruitment and range expansion (Drinkwater, 2005; Rose, 2005a,b; Wieland et al., 2009). Such predictions, however, assume adequate feeding, which has yet to occur over the full range of the stock (there is evidence of an increase in capelin in the diet of cod in the Bonavista Corridor in the past few years, G.A. Rose, unpublished data). It is suggested that the limited recovery of northern cod reflects, at least in part, a lack of response of the prey complex to the recent warming. More complex foodwebs tend to have higher compensatory dynamics in the prey complex and greater stability in the predator realm (Frank et al. 2006; 2007). Thus, they are

likely less susceptible to abrupt changes in temperature. The limiting prey for cod in this ecosystem is capelin, thus for northern cod the response of capelin to the recent warming is critical. The work leads to a prediction that future population dynamics of northern cod will be largely dependent on bottom up processes influencing primary and secondary production through the forage base (Drinkwater, 2005) and ultimately the availability of capelin (Buren et al., 2014).

Interestingly, recent studies by Obradovich (2006) and Dalapadado and Mowbray (2013) described a similar diet deficiency occurring in NL capelin as we have described for cod. In comparative analyses with the Scotian Shelf (Obradovich, 2006) and Barents Sea (Dalpadado and Mowbray, 2013), it has been demonstrated that small capelin in these ecosystems forage primarily on copepods (*Calanus finmarchicus*) but that large capelin in the other ecosystems switched to krill (*Thysanoessa inermis*) while the diet of large capelin in NL remained fixed on the smaller copepods. This finding suggests the bottleneck for capelin may be occurring at lower levels of the foodweb and demonstrates the susceptibility of northern cod to events occurring at the primary and secondary production levels of the ecosystem.

3.6 Conclusions

It is concluded that under favourable feeding conditions offshore northern cod are capable of achieving sizes, growth rates, condition levels, and mortality rates similar to those that have been resident inshore and comparable to historical norms for this stock. However, a diet deficient in capelin and dominated by shrimp is likely limiting individual performance and stock recovery. Finally, it appears unlikely that the major offshore northern cod groups will rebuild to

historical levels until this key prey species re-establishes its presence across its former range – as go the capelin, so will go the cod.

3.7 Acknowledgements

Thanks are extended to Juan Casanova, Susan Fudge, Anna Olafsdottir, Craig Knickle, Chris Canning and Diana Pike for assistance with the experiments and Gary Maillet for help with the CHN analysis. Further appreciation is extended to 3 anonymous reviewers and the handling editor Mikko Heino, whose constructive criticisms greatly improved the paper. Funding was provided by the Department of Fisheries and Aquaculture of the government of Newfoundland and Labrador and the Harris Centre of Memorial University of Newfoundland. The wild fish and data were collected under collaborative agreements with the Canada Department of Fisheries and Oceans and the Natural Sciences and Engineering Research Council of Canada Chair in Fisheries Conservation at Memorial University.

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3.9 Figures

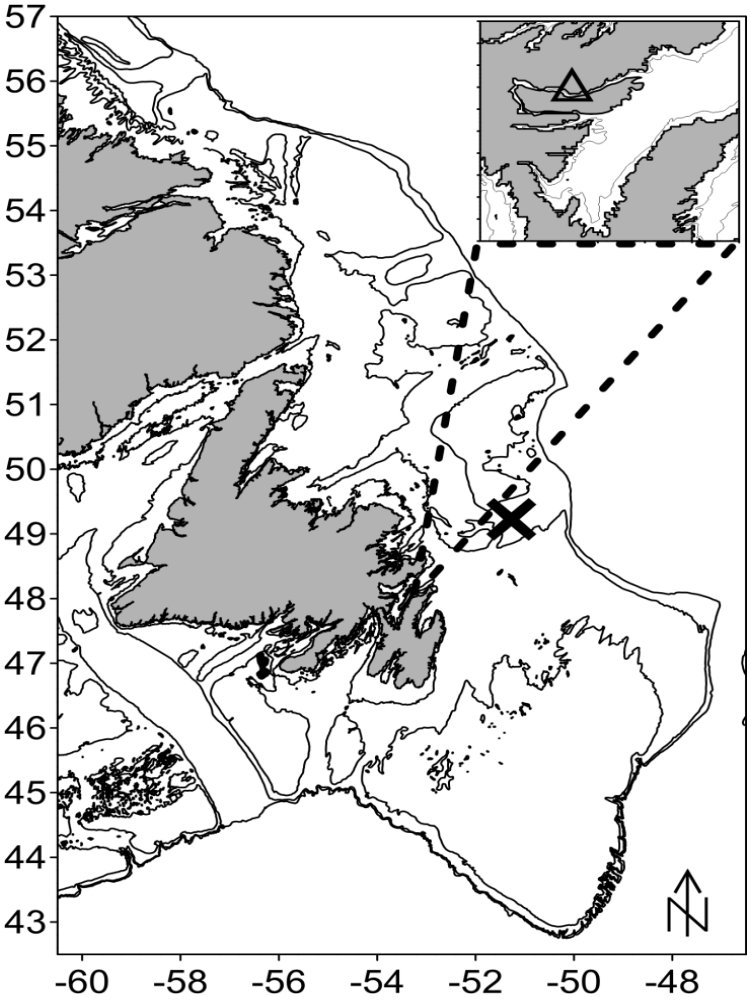

Figure 3.1. Map of the Newfoundland and Labrador shelf. Approximate locations of the Bonavista Corridor (X) and Smith Sound (Δ).

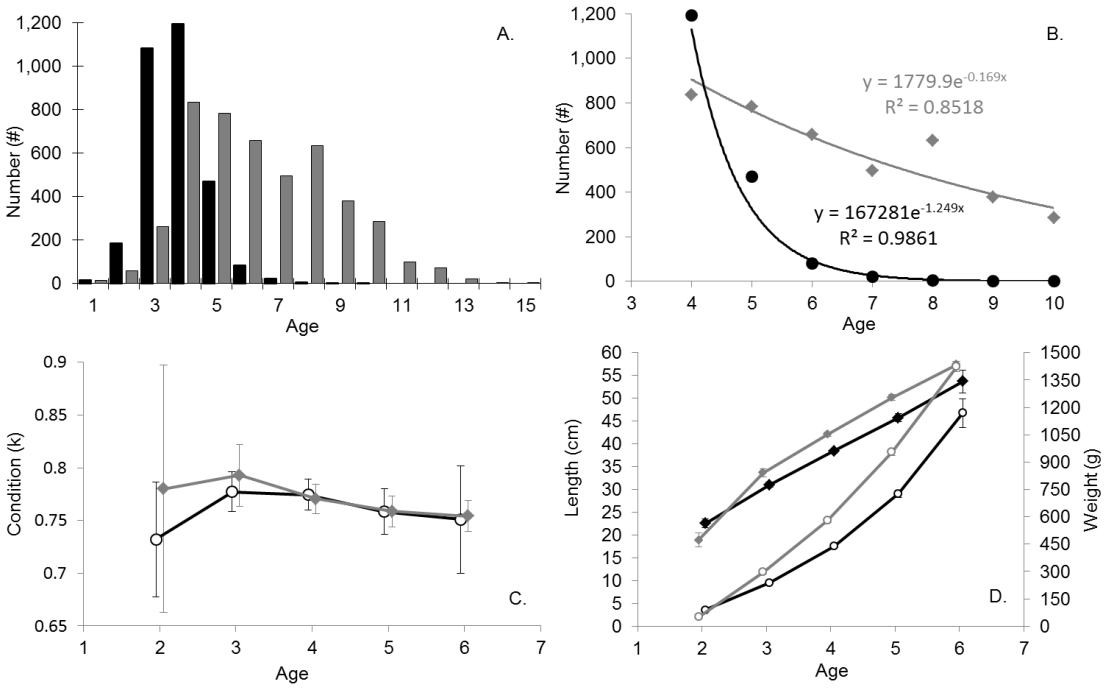

Figure 3.2. Population characteristics of wild Bonavista Corridor (black symbols) and Smith Sound (grey symbols) cod. A). Age-stratified abundance. B). Age-based mortality curves. C). Condition by age. D). Mean length (diamonds) and weight (circles) by age. Error bars represent 95% confidence intervals.

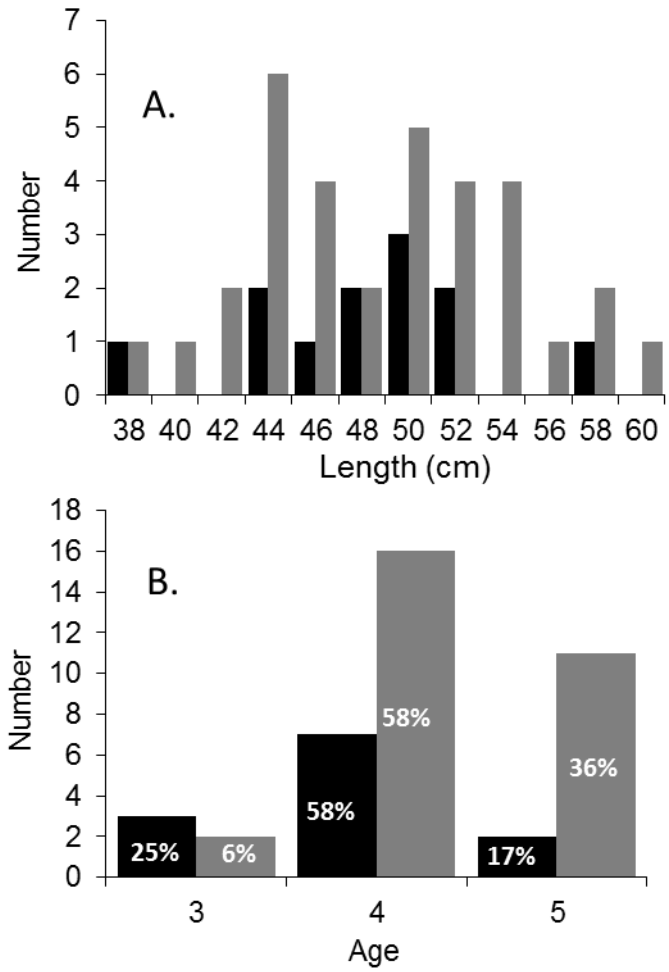

Figure 3.3. Initial experimental population characteristics for Bonavista Corridor (black bars) and Smith Sound (grey bars) cod groups. A). Length-stratified abundance. B). Age-stratified abundance.

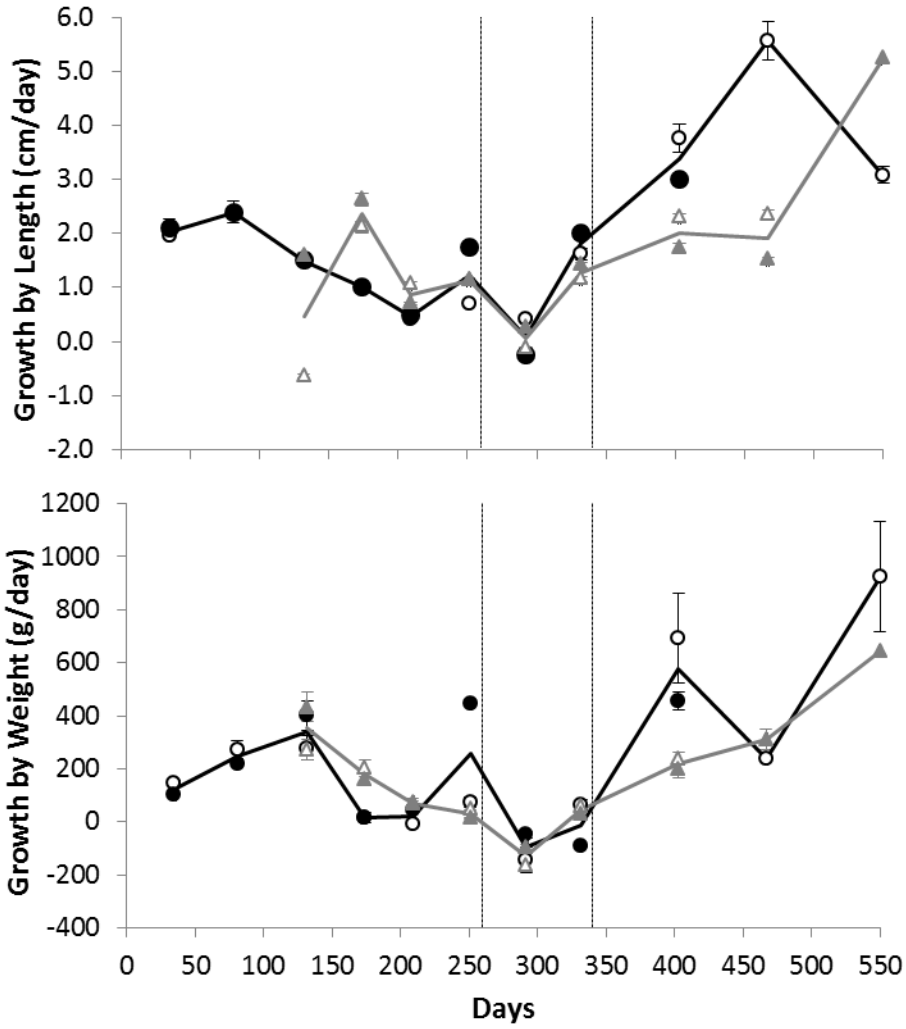

Figure 3.4. Growth of age-specific experimental cod groups by length (above) and weight (below). Bonavista Corridor (BC; black circles) versus Smith Sound (SS; grey triangles) and age 4 (open symbols) versus age 5 (solid symbols). Error bars represent 95% confidence intervals. Trend lines represent age-combined means for each group. Vertical dashed lines denote spawning period.

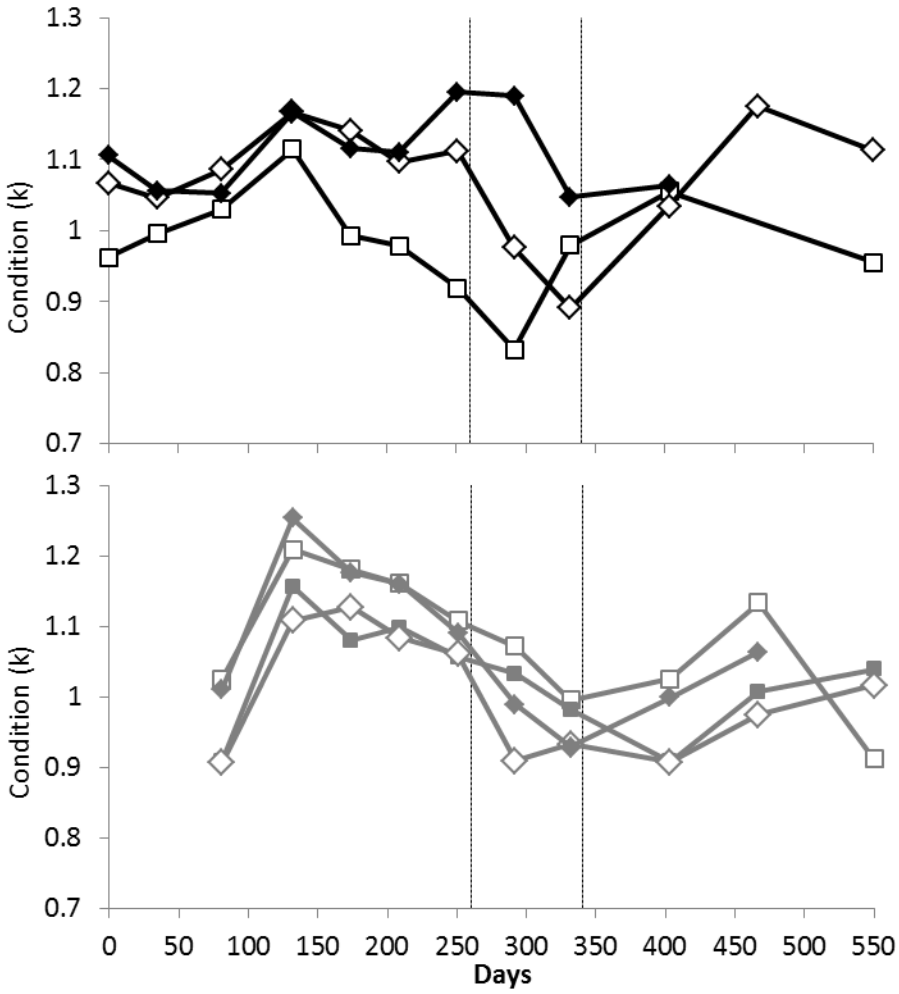

Figure 3.5. Condition of age-specific experimental cod groups for Bonavista Corridor (above; black) and Smith Sound (below; grey). Males (squares) versus females (diamonds) and age 4 (open symbols) versus age 5 (solid symbols). Vertical dashed lines denote spawning period.

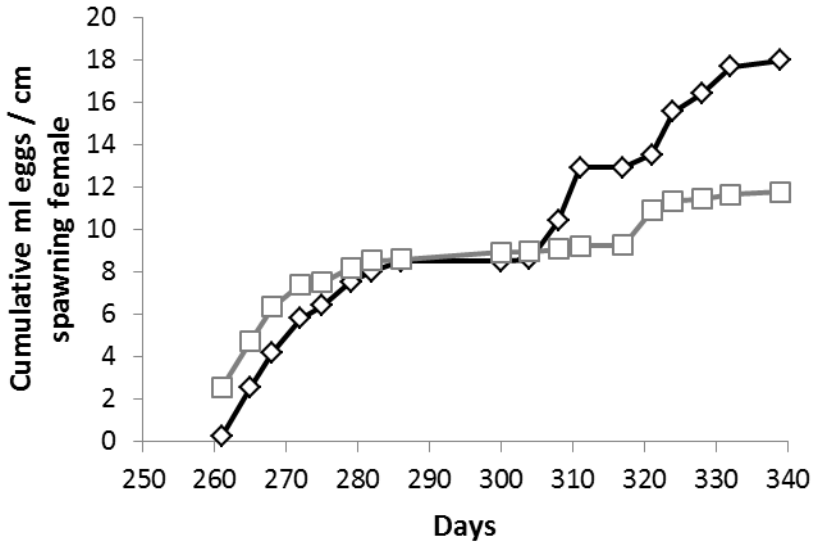

Figure 3.6. Index of reproductive output from spawning females in the Bonavista Corridor (black) and Smith Sound (grey) experimental cod groups.

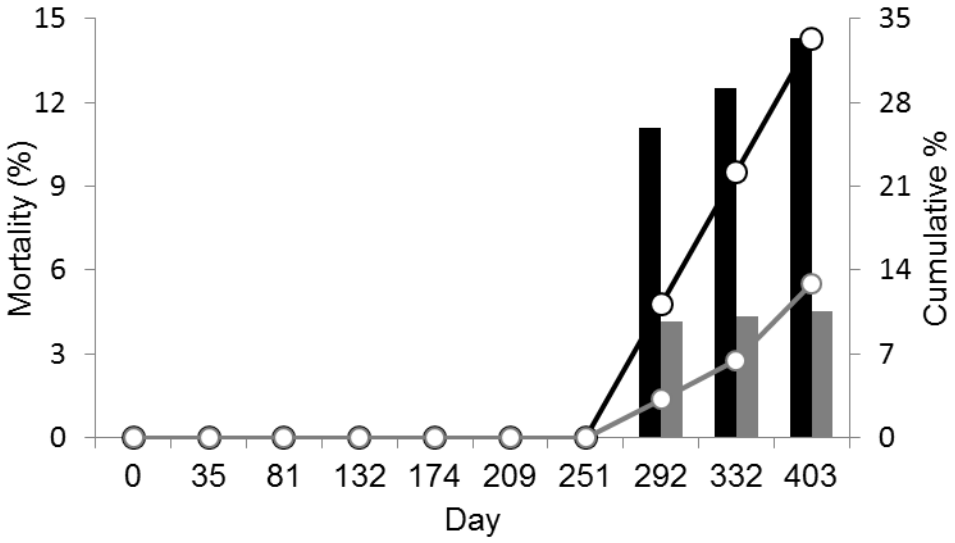

Figure 3.7. Mortality of Bonavista Corridor (black symbols) and Smith Sound (grey symbols) experimental cod groups per sampling day (bars) as well as cumulatively (lines).

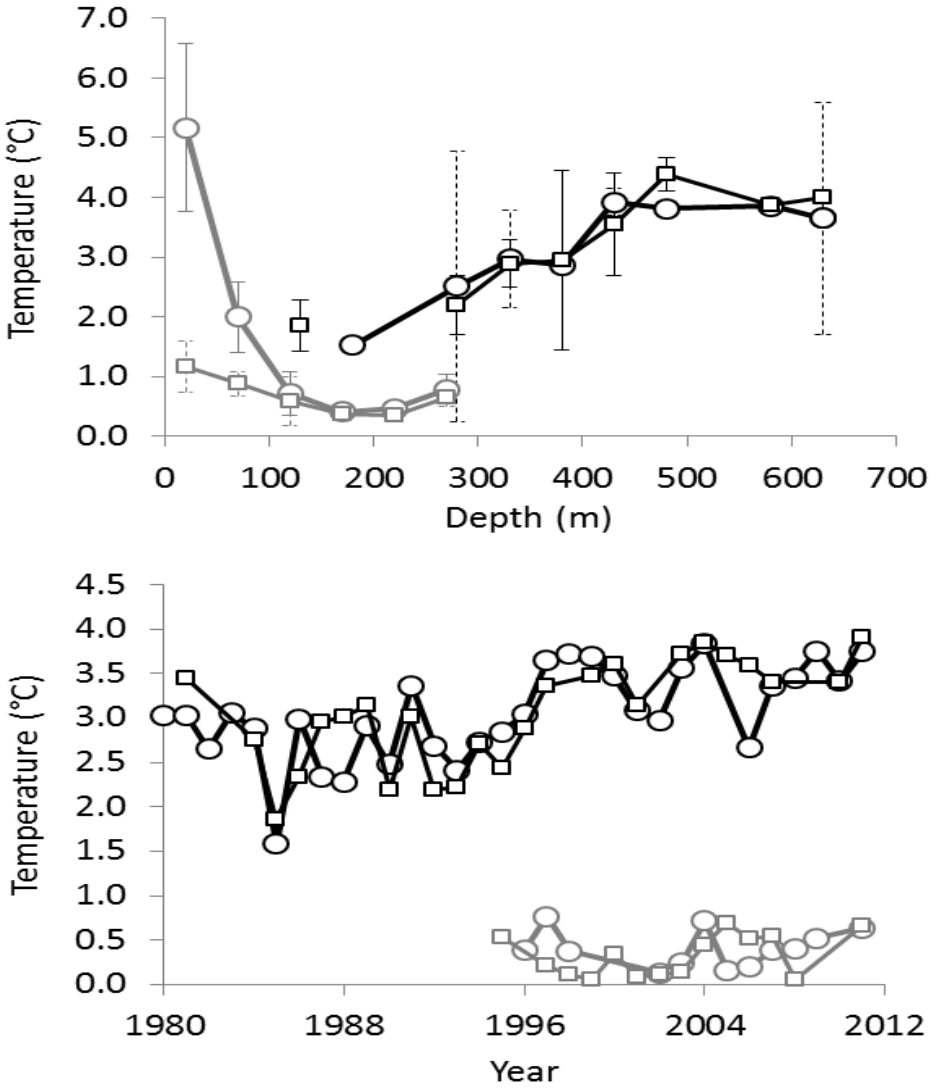

Figure 3.8. Bottom temperatures in Bonavista Corridor (black symbols) and Smith Sound (grey symbols) taken during autumn (circles) and winter (squares). Top panel shows temperature distribution by depth (pooled years). Error bars represent 95% confidence intervals. Bottom panel shows annual seasonal temperatures at the most frequently sampled depth bin in each area – 325 m in Bonavista Corridor and 175 m in Smith Sound.

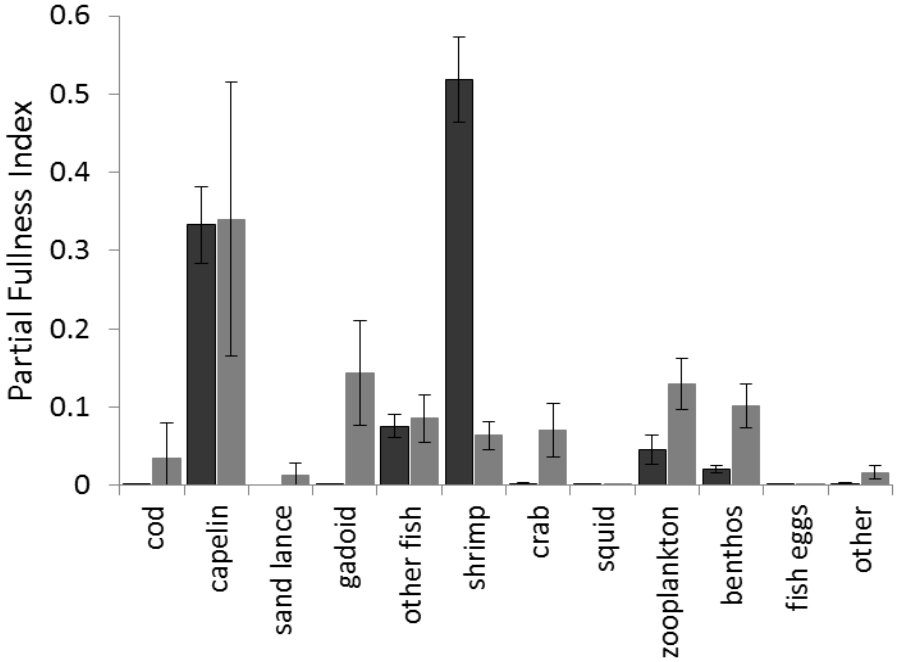

Figure 3.9. Partial fullness index of gut contents of individuals sampled from the Bonavista Corridor (black) and Smith Sound (grey) during 2002-2007. Error bars represent 95% confidence intervals.

3.10 Tables

Table 3.1. Initial sex, length (cm), and weight (kg) of Bonavista Corridor and Smith Sound cod held in captivity.

Area	Sex	Age	Length (cm)	weight (kg)
BC	F	4	49.0	1.14
BC	F	4	47.0	1.17
BC	F	4	50.5	1.34
BC	F	4	45.0	1.10
BC	F	4	46.5	1.00
BC	F	5	49.0	1.36
BC	F	5	57.0	1.95
BC	M	3	43.0	0.80
BC	M	3	44.0	0.74
BC	M	3	36.0	0.39
BC	M	4	49.0	1.29
BC	M	4	51.0	1.10
SS	F	3	39.5	0.54
SS	F	3	47.5	0.81
SS	F	4	44.0	0.81
SS	F	4	45.5	1.06
SS	F	4	59.9	1.98
SS	F	4	53.0	1.05
SS	F	4	43.6	0.80
SS	F	4	48.8	0.97
SS	F	4	52.5	1.05
SS	F	4	52.0	1.43
SS	F	5	45.8	0.93
SS	F	5	48.2	1.05
SS	F	5	52.8	1.35
SS	F	5	48.0	1.20
SS	F	5	43.8	0.88
SS	F	5	57.8	1.99
SS	F	5	44.3	0.95
SS	M	4	44.0	0.94
SS	M	4	52.0	1.49
SS	M	4	44.0	0.97
SS	M	4	38.0	0.55
SS	M	4	40.5	0.68
SS	M	4	57.0	1.71
SS	M	4	45.4	0.95
SS	M	4	43.5	0.68
SS	M	4	41.5	0.76
SS	M	4	49.4	1.32
SS	M	4	50.2	1.31
SS	M	5	49.6	1.14
SS	M	5	53.0	1.28
SS	M	5	55.0	1.61
SS	M	5	48.6	1.04
SS	M	5	51.0	1.18

Table 3.2. General Linear Model on factors affecting growth by length (cm) and weight (kg). Only main effects are shown as there were no significant interactions.

Dependent Variable	Effect	D.F.	Error D.F.	Mean Square	*F*	*p*
Length	day	1	32	11.17	7.91	0.01
	area	1	32	1.87	1.32	0.26
	age	1	32	0.0005	0.00	0.98
Weight	day	1	32	7.65	10.15	0.001
	area	1	32	0.06	0.08	0.79
	age	1	32	0.49	0.65	0.43

Table 3.3. General Linear Model on factors affecting condition (*k*).

Effect	D.F.	Error D.F.	Mean Square	*F*	*p*
day	1	344	0.28	15.24	<.0001
area	1	344	0.12	6.38	0.01
sex	1	344	0.15	8.44	0.004
age	1	344	0.003	0.16	0.69
area*sex	1	344	0.34	18.78	<.0001
sex*age	1	344	0.35	19.10	<.0001

Table 3.4. Generalized Linear Model on factors affecting mortality. Only main effects are shown as there were no significant interactions.

Effect	D.F.	Deviance D.F.	Wald Chi-Square	*p*
day	1	57	15.22	<.0001
area	1	57	3.86	0.05
sex	1	57	0.00	0.98
age	1	57	0.00	0.98

3.11 Supplementary Materials

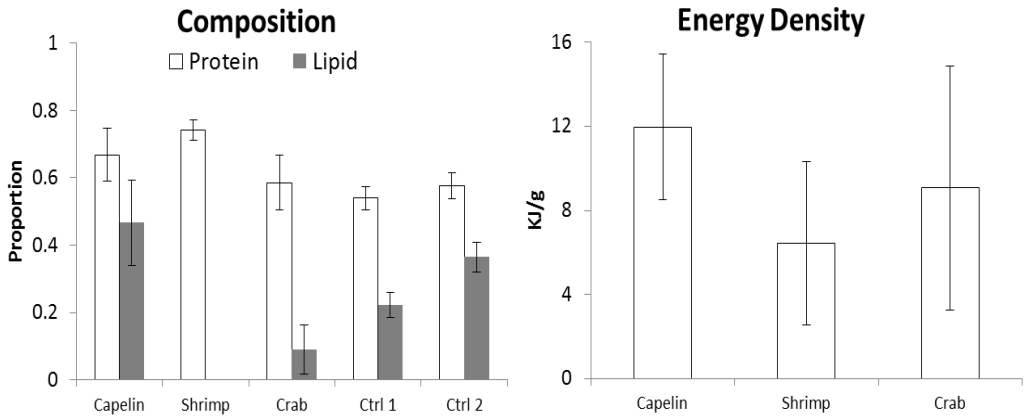

Figure 3.10. Results of Proximate composition analysis. 95% confidence intervals represented by error bars.

Table 3.4. Description of specimens used in proximate composition analysis.

Species	Measurement	Size	Sex	Details
Capelin	Total Length (cm)	17	male	
Capelin	Total Length (cm)	16	female	
Shrimp	Carapace Length (mm)	22	female	
Shrimp	Carapace Length (mm)	22	female	
Shrimp	Carapace Length (mm)	24	female	
Shrimp	Carapace Length (mm)	16	male	
Shrimp	Carapace Length (mm)	21	female	
Crab	Carapace Width (mm)	57	female	old-shell
Crab	Carapace Width (mm)	32	male	new-shell

Table 3.5. Statistical testing of wild population metrics.

Dependent Variable	Model	D.F.	Error D.F.	Mean Square	f	p
Age	group (weight=n)	1	7737	28983.37	3131.38	<.0001
Mortality (n)	age*group	2	11	655388.39	14.81	<.001
Condition	age*group	2	5631	0.12	16.97	<.0001
Length	age*group	2	5632	243733.07	12671.9	<.0001
Weight	age*group	2	5636	540.10	8195.03	<.0001

Table 3.6. Statistical testing of initial experimental population metrics .

Dependent Variable	Model	D.F.	Error D.F.	Mean Square	f	p
Age	group (weight=n)	1	4	1.32	0.35	0.59
Length	group (weight=n)	1	17	2.34	0.03	0.86

Table 3.7. Mean lengths and weights of age-specific cod in each group by sampling day. 95% confidence intervals given by ±.

	Bonavista Corridor												Smith Sound											
	Age 3			Age 4			Age 5			Age 3			Age 4			Age 5							
Day	cm	±	g	±	cm	±	g	±	cm	±	g	±	cm	±	g	±	cm	±	g	±	cm	±	g	±
0	43.5	0.4	711	27	48.3	1.3	1162	71	53	3.4	1656	250												
35	44.5	0.4	811	79	50.3	1.3	1308	111	55.1	2.8	1758	142												
81	45	0.9	838	147	52.7	1.6	1580	210	57.5	2.1	1979	8	43.5	4.0	672	273	47.6	6.8	1079	224	49.8	2.5	1216	184
132	46	0.9	895	234	54.1	2.1	1859	300	59	1.7	2380	4	46.3	4.8	1132	932	47	2.8	1351	191	51.4	2.3	1650	207
174	48.5		1086		55.1	2.6	1877	334	60	1.3	2396	60	48.5	3.5	1203	996	49.1	2.5	1555	241	54	2.4	1811	241
209	48.5		1048		55.6	2.6	1870	365	60.5	1.3	2441	86	48	5.0	1247	1034	50.2	2.5	1622	262	54.8	2.3	1886	273
251	48.5		976		56.3	3.0	1945	450	62.3	0.7	2885	131	49.3	5.3	1254	972	51.3	2.4	1674	253	55.9	2.4	1901	275
292					56.7	3.6	1802	613	62	3.4	2836	250	50.3	4.8	1025	462	51.2	2.5	1511	216	56.1	2.3	1805	239
332					58.3	3.9	1868	525	64	2.8	2744	142	50.3		1019		52.3	2.3	1573	189	57.5	2.3	1834	266
403					62.1	4.5	2561	621	67	2.1	3200	8	55		1006		54.6	2.2	1810	189	59.3	2.9	2032	331
467					67.7	4.4	2800	71									56.9	2.2	2298	266	60.8	2.6	2344	296
550					70.8	3.5	3723	111																

Table 3.8. Condition of age-specific cod in each group by sampling day. Upper and Lower 95% confidence bounds indicated by 'up' and 'low'.

	Bonavista Corridor										Smith Sound									
	Male				Female						Male				Female					
	Age 4				Age 4				Age 5		Age 4				Age 4				Age 5	
Day	Mean	up	low		Mean	up	low		Mean	up	low		Mean	up	low		Mean	up	low	
0	0.96	2.68	-0.75		1.07	1.19	0.94		1.11	1.78	0.43									
35	1.00	2.70	-0.71		1.05	1.22	0.88		1.06	2.19	-0.08									
81	1.03	2.38	-0.32		1.09	1.24	0.93		1.05	2.72	-0.62		1.03	1.08	0.97		0.91	0.96	0.86	
132	1.11	3.16	-0.93		1.17	1.35	0.98		1.17	2.64	-0.31		1.21	1.29	1.13		1.16	1.25	1.06	
174	0.99	2.40	-0.41		1.14	1.30	0.98		1.12	2.59	-0.36		1.18	1.24	1.13		1.08	1.20	0.96	
209	0.98	2.30	-0.35		1.10	1.23	0.96		1.11	2.74	-0.52		1.16	1.20	1.12		1.10	1.22	0.98	
251	0.92	2.21	-0.37		1.11	1.31	0.91		1.19	1.42	0.97		1.11	1.17	1.05		1.06	1.21	0.90	
292	0.83	2.53	-0.87		0.98	1.16	0.79		1.19				1.07	1.11	1.03		1.03	1.17	0.89	
332	0.98				0.89	1.06	0.72		1.05				1.00	1.03	0.96		0.98	1.12	0.85	
403	1.05				1.03	1.23	0.84		1.06				1.03	1.09	0.96		0.91	1.08	0.74	
467	0.96				1.17								1.13	1.21	1.06		1.01	1.21	0.81	
550					1.11								0.91				1.04			

	Smith Sound				
	Female				
	Age 4				Age 5
Day	Mean	up	low		Mean	up	low
0							
35							
81	0.91	1.03	0.79		1.01	1.08	0.95
132	1.11	1.27	0.94		1.25	1.46	1.04
174	1.13	1.24	1.01		1.18	1.28	1.07
209	1.08	1.19	0.98		1.16	1.28	1.04
251	1.06	1.13	0.99		1.09	1.22	0.96
292	0.91	1.03	0.78		0.99	1.09	0.89
332	0.93	1.00	0.86		0.93	1.08	0.78
403	0.91	0.96	0.85		1.00	1.16	0.84
467	0.97	1.15	0.80		1.06	1.24	0.89
550	1.02	2.96	-0.93				

Table. 3.9. Captive versus wild comparisons of mean lengths and weights for ages 5 and 6 cod. (Captive ages determined as age 5=age 4+332d and age 6=age 5+332d).

		Length (cm)				Weight (g)			
Group	Age	wild	captivity	Δ = (captivity - wild)	% = (Δ /wild)*100	wild	captivity	Δ = (captivity - wild)	% = (Δ /wild)*100
SS	5	50.13	52.3	2.17	4.33	955	1573	618	64.71
SS	6	57.45	57.5	0.05	0.09	1424	1834	410	28.79
BC	5	45.75	58.3	12.55	27.43	727	1868	1141	156.95
BC	6	53.71	64	10.29	19.16	1168	2744	1576	134.93

Chapter 4

Spawning delays of northern capelin (*Mallotus villosus*) and recovery dynamics: a mismatch with ice-mediated spring bloom?

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Chapter 4 builds upon Chapter 3 which determined a capelin deficient diet was contributing to delayed northern cod recovery. This chapter examines factors affecting capelin productivity in the post-collapse period. Using a broad suite of data sources, the study finds that poor productivity during most of the post-collapse period was related to a mismatch with the spring bloom. Increased productivity in the stock in recent years is shown to be associated with an increase in preferable and total zooplankton abundance and a decreasing trend in the mismatch with the spring bloom. A central mechanism underlying the improvements is reduced ice coverage associated with warming conditions, which produces a more favourable zooplankton community for first feeding. Thematically, the study complements the two previous research chapters in demonstrating that bottom-up processes near the base of the foodweb underpin poor post-collapse capelin performance, and by extension northern cod.

4.1 Abstract

The capelin stock off the northeast coast of Newfoundland and southern Labrador collapsed in the early 1990s along with most of the finfish community. Among a host of concomitant physical and behavioural changes was the onset of delayed spawning, a phenomenon that has persisted for over two decades. From the mid-1990s onward, the Newfoundland and Labrador shelf has been warming with ice levels reduced in most years, generally leading to earlier spring plankton blooms. The delayed spawns and earlier blooms have resulted in an increased mismatch between plankton production and larval emergence, which we hypothesized could result in reduced early-life survival and prolonged stock recovery. Among indices associated with the mismatch, including time between blooms and spawning, composition and abundance of zooplankton during early ontogeny, and sea surface temperature and ice coverage, potential linkages were found with first year capelin survival. Increased capelin productivity in recent years has been associated with an increase in preferable and total zooplankton abundance and a decreasing trend in the mismatch with the spring bloom. A generalized linear model incorporating a match-mismatch index and stage I-IV calanus copepods explained 82% of the variance associated with annual age 0 capelin abundance estimates since stock collapse. A central mechanism underlying improvements in capelin productivity appears to be a general reduction in ice coverage associated with a recent warm oceanographic regime that reached record high levels in 2011.

4.1.1 Keywords: Capelin, Newfoundland and Labrador, Spring Bloom, Zooplankton, Match-Mismatch

4.2 Introduction

Capelin (*Mallotus villosus*) is the most important forage species in the waters off Newfoundland and Labrador (NL) for many species of finfish, seabirds, and marine mammals (Montevecchi and Piatt, 1984; Rose and O'Driscoll, 2002; Davoren et al., 2007). A thirty-fold reduction in capelin abundance occurred in the Northwest Atlantic Fisheries Organization (NAFO) Divisions 2J3KL during 1991 (hereafter the northern capelin, Figure 4.1) (Bakanev, 1992). This rapid decline was accompanied by shifts toward later spawning times (i.e. July vs. May), smaller sizes, earlier maturation, and a reduction in individual condition (DFO, 2013). These changes, along with low abundance, have persisted for the past two decades, abating somewhat only in the last few years (DFO, 2013; 2014).

The reasons for persistent poor recruitment, low abundance, and delayed spawning have remained speculative (Carscadden et al., 2001). Poor condition has been hypothesized to relate to poor feeding, in particular a lack of euphausiid prey for larger (age 2+) capelin (Dalpadado and Mowbray, 2013; Obradovich et al. 2013). Diet deficiencies could also relate to smaller size, higher mortality, and later spawning, but the lack of any strong year classes in more than two decades suggests other factors may also be involved in curtailing long-term recruitment to this stock (Buren et al., 2014).

Capelin have a distinct life history in NL waters in which beach spawning is a common trait, although inter-tidal and demersal spawning also occurs (Davoren et al., 2006; 2007). Mortality in the earliest life stages is widely held to be an important determinant of year class strength.

Even prior to emerging from the beach, variability in air and water temperature, solar radiation, and wind direction can influence egg survival (Leggett et al., 1984; Frank and Leggett 1981a,b; 1982a;b). Once released into the pelagic realm, food availability likely impacts survival of emergent larvae (Leggett et al., 1984). Accordingly, in keeping with the match-mismatch theory of recruitment variation (Cushing, 1969; 1990), the timing of the early pelagic phase with respect to food production could be paramount in determining year class strength.

As in most temperate marine ecosystems, the primary food and energy production event along the NL shelf is the spring bloom (Head and Pepin, 2010). Larvae emerging in late summer or early fall may miss conditions conducive to survival and growth (Frank and Leggett, 1982b). In both the northwest and northeast Atlantic, the diet of young capelin has historically been dominated by small copepods (Carscadden et al., 2001; Melle et al., 2004), which are typically most abundant following the initial phytoplankton production phase of the bloom. We postulated that the later spawning of northern capelin over the past two decades has led to poorer recruitment and created a 'mismatch pit' in which stock productivity has been held at a low level.

In this paper, our primary objective was to investigate if a mismatch between spawning and subsequent larval release with the spring bloom could explain variations in year-class strength in the northern capelin stock. Using a diverse set of data sources dating back to 1970, the relationships among capelin spawning and spring bloom timing, zooplankton community structure, and capelin year class strength were examined.

4.3 Methods

4.3.1 Spring Bloom Dynamics

Data from satellite systems monitoring sea surface conditions were provided by the Bedford Institute of Oceanography (Dartmouth, Nova Scotia). Moderate Resolution Imaging Spectrodiometer (MODIS) satellite data, collected continuously from January 2004 until December 2013, were combined with Sea-viewing Wide Field-of-view Sensor (SeaWiFS) satellite data from September 1997 until December 2009 to construct a composite time series of surface chlorophyll *a* (*chla*) concentrations across four statistical sub-regions in Newfoundland and Labrador (Petrie Boxes, Figure 4.1). Chlorophyll concentration was determined by correlating satellite observations of ocean colour with known concentrations from water sampling (see http://science.nasa.gov/earth-science/oceanography/living-ocean/remote-sensing). Basic statistics (mean, range, standard deviation, etc.) were developed from two week average composites in these sub-regions, with an average value of *chla* used during the overlap period of the satellite system operation. Data gaps greater than one month in duration, such as when sea ice was present, were excluded from analyses.

A shifted Gaussian function of time model developed by Zhai et al. (2011) was employed to describe the characteristics of the seasonal cycle of phytoplankton production based on the combined satellite data, with midpoints of the two week intervals representing days in the analysis. Five different metrics were computed using the satellite composite data from January through the end of August each year, including background *chla* concentration (mg m^{-3}), the

integral of *chla* under the Gaussian curve (mg m^{-2} d^{-1}), timing of the spring bloom peak (Calendar day), duration of the bloom cycle (days), and bloom initiation time (calendar day), covering the period 1998-2013 (Table 4.1). Bloom start and end times were defined as temporal points along the Gaussian curve when 20% of the maximum amplitude of the bloom occurred, with the difference between start and end times representing bloom duration.

Initial correlation analyses with environmental variables of spring-winter surface temperatures and ice dynamics revealed that peak bloom timing was the bloom index most closely associated with physical oceanographic variables (Table 4.2), thus it was the focus of the present study. This index of bloom timing was defined as the day when highest *chla* concentrations occurred during January through late August of a given year.

An index of historical bloom timing was developed through exploratory regression analyses with sea surface temperature (SST) and sea ice dynamics. The peak timing data were compared with winter-spring sea surface temperatures (Jan.-Apr.) from the Northeast NL shelf and St. Anthony Basin Petrie Boxes (Figure 4.1), which corresponded most closely with the distribution of the capelin stock, as well as the annual areal coverage of sea ice along the shelf, the southernmost extent of ice cover, and the day ice retreat began each year. The three ice indices were developed and provided by Buren et al. (2014), with the time series ending in 2010. All indices were linearly or near-linearly and significantly associated with satellite-observed peak timing of the spring bloom from 1998-2010, but the closest association occurred with the southernmost extent of ice (r^2*=0.39, f=6.91, p=0.023;* Table 4.3). Stemming from this, we

updated the ice latitude index for the most recent three years following their criteria and referencing historical ice maps from Environment Canada. The resulting 1998-2013 regression model (peak day=-3.6896*ice latitude + 294.37) was used to hind-cast peak bloom day back to 1970 based on the ice extent data. Consequently, the entire 1970-2013 peak bloom index was based on this regression equation.

To validate the utility of the hind-casted peak bloom index as a reliable proxy it was compared against vertically averaged water temperature (all depths) from January to April at Station 27, the longest-running oceanographic monitoring site in the Northwest Atlantic, located along the approach to St. John's Harbour (Figure 4.1). The cold water transported by the Labrador Current, known as the Cold Intermediate Layer (CIL), extends throughout the water column at this station due to its location on the relatively shallow (176 m depth) broad northern region of the Grand Bank. Significance testing between the proxy peak bloom timing index and Station 27 water temperatures was initially conducted using simple linear regression on data transformed to first differences ((y+1)-y). The transformation was done to introduce stationarity in the time series' because investigation with a Durbon Watson test revealed a positive first-order autocorrelation process in the peak bloom timing index ($p<0.01$).

Data on zooplankton community structure were acquired from the Continuous Plankton Recorder (CPR). The CPR program is operated by the Sir Alister Hardy Foundation for Ocean Sciences (SAHFOS – www.sahfos.ac.uk). Using the CPR, plankton samples were taken from ship-towed collectors on commercial container vessels operating throughout the North Atlantic.

Plankton samples were captured on a moving band silk mesh (width=10 cm, mesh=270 µm) and assigned to 10 nautical mile (nm) scales of resolution along vessel tow paths (further details on CPR sample collection and quantification are reported in Hays and Lindley (1994) and Richardson et al. (2006). Along the NL Shelf, data were available for Divisions 3K and 3L (Figure 4.1) dating back to 1960, although there was a gap in collections between 1979 and 1991, so only data since 1991 were used in this study. Most zooplankton specimens were distinguished to the taxa level, but small calanoid copepods were ambiguous and grouped as *Calanus stage I-IV (CI-IV)*. These are thought to consist mainly of *Calanus finmarchicus (C. fin.),* as they are the dominant calanoid copepod present along the NL shelf (further details on classification of zooplankton taxa are included in Head and Pepin [2010]). Apart from *CI-IV* and *C. fin.,* the most common groups captured and presented in the study include *Calanus glacialis, Calanus hyperboreus,* Copepod nauplii*, Para-pseudocalanus* spp*., Oithona* spp*.,* Hyperiid amphipods*,* and Euphausiids*.* Note *Para-psedocalanus* belong to the genus *pseudocalanus* as opposed to the *calanus* genus of other copepods detailed here.

Due to the opportunistic nature of specimen collections, data from the CPR were found to be temporally inconsistent across the study period. Accordingly, taxon-specific abundance estimates were derived through multiple univariate general linear models (GLM) using month as an explanatory variable to produce annual least square means (LSM). All taxa were combined to produce standard errors, thus the error terms were shared across taxa. The LSM abundance estimates from four select taxa (*CI-IV, Para-pseudocalanus, Oithona* spp*., and* Copepod nauplii), which due to their consistently high abundance and small sizes (Melle et al., 2004) were

deemed to have the highest potential to be consumed by early-life stages of capelin, were focused on in correlation (Pearson coefficients) comparisons with peak bloom timing and capelin year class strength in assessing the phenological associations of zooplankton with bloom timing and capelin abundance. Significance testing of the pairwise relationships was conducted using simple linear regression, with a priori screening for first-order autocorrelation in the data series conducted with Durbin-Watson tests and normality and homoscedasticity assessed by examination of histograms and residuals. For interpretation of significance, the significance level was adjusted to control for familywise error rate associated with multiple comparisons using a Šidák correction ($1-(1-\alpha)^{1/n}$), where n is the number of independent tests (4) and α is the nominal significance level chosen. Relationships testing significant at *p=0.0260* (nominal *p=0.10*) were viewed as significant as the Šidák corrected level of nominal *p=0.05* (*p=0.0127*) was deemed too stringent in allowing variables to emerge as significant.

4.3.2 Interactions of Key Processes

An index of spawning time employed in assessments of the Div. 2J3KL capelin stock (DFO, 2013) was used along with the peak bloom timing index to assess the temporal association of capelin spawning and the spring bloom. These spawning time data were from Bryant's Cove, Conception Bay (Figure 4.1), and represent the longest running series of beach spawning times available, dating back to 1980 (Table 4.1). The peak spawning day was determined by substrate surveys and represented the day with the densest amount of eggs present in beach core samples.

A ‘Match-Mismatch Index (MMI)’ was calculated and defined as the number of days between peak bloom and spawning times each year when data were complete. To assess the importance of the phenological association of spring bloom and capelin spawning, the MMI was compared to an index of capelin year class strength. The year class strength index was developed from a spring acoustic survey conducted in Div. 3KL in most years since the early 1980s (Miller and Carscadden, 1991; DFO, 2013). The surveys essentially measure the relative abundance of age 2+ capelin along the northern portion of the Grand Bank (predominately in Division 3L) in the spring of each year. They are conducted in May from the Canadian Coast Guard Research trawler *Teleost*. There have been numerous changes in survey transect design and areal coverage since the late 1980s, with a set of core strata introduced for analysis in 2009. Acoustic backscatter was attributed to species using echogram characteristics and biological fish attributes were determined from complementary mid-water trawl catches. Abundance estimation was done by age, using a Monte Carlo approach on length-based (i.e. age proxy) target strengths. For unknown reasons relatively few fish younger than age 2 have been present in the survey data for the past two decades (for further survey details see Mowbray, 2014). The age-specific abundance estimates from the survey were provided by the Pelagics Section of DFO in St. John’s (see DFO, 2013). The year class index used in this study was the natural log-transformed abundance estimates of age 2 fish from the acoustic survey. It was lagged by two years (back to age 0) in comparisons with the MMI and zooplankton community. This approach is supported by the coherence of 0-group survey estimates from a long-term monitoring site in Trinity Bay to age 2 abundance in the offshore acoustic surveys throughout the 2000s (DFO, 2011).

Simple cross-correlation (Pearson coefficients) analysis was initially conducted to identify important pathways among exogenous environmental input variables and endogenous response variables in the ecosystem. These included Jan.-Apr. sea surface temperature (SST) from the Northeast Shelf Petrie Box (Figure 4.1), the annual extent of sea ice (ICE), the peak timing of the spring bloom index (SB), the abundance of *CI-IV* (CIIV), the abundance of *Oithona* spp. (OI), the match-mismatch index (MMI), and capelin year-class strength (age 0 abundance (AB)). Significance of each correlation was assessed at the conventional $p=0.05$ level. A scatter plot matrix embedding distribution histograms for each variable along with 95% probability ellipses was presented to visually assess the shape of individual relationships.

A generalized linear model (GLM) using the two explanatory variables identified to have significant influence on capelin year class strength in the cross-correlation analysis, the abundance of *CI-IV* and the MMI, was run in SAS Enterprise Guide Version 5.1 ('genmod'). Generalized linear models contain an inherent linear predictor, a monotonic link function that describes how the mean depends on the linear predictor, and a variance function that describes how the variance depends on the mean. They require no assumption that errors are independent, have equal variance, or are normally distributed. GLMs are commonly used in modeling cluster-correlated data. In the case of the NL capelin stock a 'period' effect was present in the data, with high pre-collapse abundance and low post-collapse abundance, thus the GLM was deemed a robust selection to handle any potential periodic effects in the data. The model tested the explanatory variables as both main and interaction effects on the

dependent variable of the natural log-transformed age 0 capelin abundance index. It was programmed as a Type III analysis using an identity link function for a normal distribution.

4.4 Results

4.4.1 Spring Bloom Dynamics

Cold and ice-laden conditions were associated with delayed spring blooms, with annual changes in the peak timing proxy inversely related to temperature at Station 27 (r^2*=0.37, f=23.60, p<0.0001*) (Figure 4.2). Although both metrics have undergone oscillations since the early 1970s, and annual variability has been higher since the late 1990s, temperatures have generally been warmest and blooms earliest in recent years. Three of the earliest blooms, on calendar days 111-115 (April 21-25), have occurred in the past four years.

The period since the capelin collapse and re-establishment of CPR data collections in 1991 was characterized by relative stability in overall zooplankton abundance, similar to historic levels, from about 1991-2002 (Figure 4.3). A period of relatively low overall abundance occurred from 2003-2008, but zooplankton abundance has increased to near the highest observed levels in the past four years.

Zooplankton community composition along the NL shelf has been consistently dominated by *C. fin., CI-IV,* Copeopd Nauplii*, Para-pseudocalanus*, and *Oithona* spp. Of these, all but *C. fin.* are likely to be small enough to be consumed by early life capelin stages. All dominant taxa have been at relatively high levels in the past four years.

CI-IV and *Para-pseudocalanus* were negatively associated with spring bloom timing (Figure 4.4a;b) and positively associated with capelin year class strength (Figure 4.5a;b) since 1991. By annual LSM estimates, *CI-IV was* strongly correlated and significantly related (*p<0.0260*) to both capelin abundance and spring bloom timing in the extended time series, and *Para-pseudocalanus* was also significantly related to capelin abundance in the extended time series (Figures 4.4-4.5). The insignificant relationships in the shorter time series could reflect a tighter coupling of these taxa with capelin abundance in recent years or improved precision with more data.

Converse to *CI-IV* and *Para-pseudocalanus*, *Oithona* spp. and Copepod Nauplii showed either no or positive associations with bloom timing (Figure 4.4c;d) and no or negative associations with capelin abundance (Figure 4.5c;d). *Oithona* sp*p.* were more tightly coupled with both variables than Copepod Nauplii, with significant (*p<0.0260*) relationships occurring between *Oithona* spp*.* and both variables in the shorter time series (1991-2009). Interestingly, a general pattern occurred with the strength of correlations and significance of the relationships eroding in the extended time series. This reflects a divergence in trends since 2009, whereby both taxa have fell out of phase and increased in abundance coincident with earlier blooms (Figure 4.4c;d) and increased capelin abundance (Figure 4.5c;d).

4.4.2 Interactions of Key Processes

Associations of surface temperature and in particular annual ice extent with spring bloom timing were strong (Figure 4.6). In turn, the spring bloom showed negative associations with the abundance of *CI-IV* as well as the MMI. Note that any significance in the relationships among the MMI, spawning day, and spring bloom timing reflect redundancy in the variables due to the incorporation of bloom timing into the calculation of the MMI. Age 0 capelin abundance was significantly related *($p<0.05$)* to the MMI (Figure 4.6-4.7) and *CI-IV* in annual abundance estimates (Figure 4.6).

The generalized linear model revealed that the interaction of *CI-IV* abundance and the MMI exerted a highly significant influence over the year class strength of capelin (Table 4.4, $\chi^2=13.17$, $p=0.0003$). The estimated model was assessed as a good fit to the data based on the ratio of the Pearson χ^2 fit statistic to the degrees of freedom (=1.5 [not shown]), with a close association to 1 indicating a good fit. The model, defined as:

(Ln Abundance= (*CIIV**41.04)+(MMI*0.3713)+((*CIIV**MMI)*-0.4854)-30.054)

explained 82% of the variance in the acoustic survey abundance estimates since stock collapse (Figure 4.8) and predicted little change from the observed 2012 level in 2013, which would translate to little change in age 2 abundance in 2015.

4.5 Discussion

4.5.1 Spring Bloom Dynamics

Our results showed that sea ice was strongly associated with bloom timing and subsequent ecosystem processes affecting capelin abundance, a result consistent with modeling by Buren et al. (2014). The NL shelf is an ice edge region where ice coverage and retreat represent large-scale forcings affecting the phytoplankton bloom (Harrison et el., 2013). Inter-annual variability in ice retreat is tightly coupled with bloom timing (Wu et al., 2007; Harrison et al., 2013), with warm conditions generally producing early blooms (Head et al., 2013). Primary production is limited by light and nutrients (among other variables), but with nitrate and other nutrients only mildly limiting in this area, the relationship with light is especially key (Gnanadesikan et al., 2014). Levels of photosynthetic active radiation (PAR) are generally weak in spring (Wu et al., 2007), and dissipating ice serves to relieve light limitation on the mixed layer in triggering the bloom. The water rapidly stratifies in association with the melting ice, the mixed layer shoals, and secondary production becomes enhanced as the major energy generation phase of the ecosystem ensues.

Bloom timing was negatively associated with *CI-IV* and *Para-pseudocalanus*, which were positively associated with capelin abundance. Broadly speaking, up until 2009 two 'states' of zooplankton community composition had emerged; a 'temperate state' dominated by preferential *CI-IV and Para-pseudocalanus* and a 'cold state' dominated by apparently less preferential taxa such as *Oithona* spp. It is unknown to what degree emergent capelin select for or against any given prey, but our analysis strongly suggests the 'temperate state' to be more favourable to increased early-life survival due to the long-term association of age 0 capelin abundance with *CI-IV* and *Para-pseudocalanus* copepods. Nonetheless, after 2009 the relative

abundance of other potential prey taxa, specifically *Oithona* spp. and Copepod Nauplii, increased coincident with early blooms and fell out of phase with the two decade long trend. Why this occurred is not known but it supported an overall increased abundance of potential prey along the NL shelf that coincided with an increase in capelin abundance. In the Norwegian Sea, as in the NL shelf ecosystem, upper trophic level processes largely hinge on the success of capelin, and *C. fin.* is deemed the 'star actor' of the ecosystem (Melle et al., 2004). Young *C. fin.* stages constitute the main food for larvae of most commercial fish stocks and older stages represent the main food of large capelin. The small cyclopoid copepods *Oithona* spp., dominated by *O. similis*, are most abundant in late summer and autumn (Melle et al., 2004), thus generally occur later than capelin spawning times when *CI-IV* is more commonplace. Along with the phenology of zooplankton community composition and bloom timing, another factor that could temporally affect the match-mismatch is egg development times, with development delayed in cold conditions (Leggett et al., 1984; Frank and Leggett 1981a;b; 1982a;b). It holds that delayed larval emergence in cold conditions could further exacerbate the mismatch from apparently preferential prey species associated with early blooms.

On the Newfoundland and Labrador shelf, although the recent high levels of *CI-IV* that have accompanied the warm period have likely been beneficial to promoting increased survival of young capelin, it appears that after 2009 the additional compounding benefit of increased abundance of 'cold state' taxa could also be driving improved capelin abundance. Our study lacks diet samples from early-life exogenous feeding to supplement the findings of increases in zooplankton contributing to increasing capelin abundance, but a survey conducted in mid-late

August in Trinity Bay (Figure 4.1) during 2013 showed *Oithona similis* to be the primary prey of capelin ranging from about 3-15 mm in length (personal communication, Timothée Govare, Memorial University of Newfoundland). These results support the notion that overall increases in zooplankton abundance and not just historically preferred species could be supporting an improvement in the northern capelin stock. If capelin continue to spawn late, having a 'buffer' of such later-emerging zooplankton species could be of great benefit. Overall, there appears to have been an increase in the total abundance of potential zooplankton prey available to emergent capelin in recent years under warm and early bloom conditions.

Our results indicate that early spring plankton blooms may be favourable for capelin, but that spawning times must be in-sync with the bloom to support high productivity. Nonetheless, although the mismatch of capelin spawning times with the spring bloom has been closing, spawning remains delayed relative to historical norms. Thus, capelin may still not be fully capitalizing on the most favorable opportunities for early-life feeding.

Early blooms appear most beneficial for high *CI-IV* and *Para-pseudocalanus* abundance, two taxa which were historically preferential in supporting young capelin. Head et al. (2010; 2013) suggest that (warm) early bloom conditions lead to advanced development in *C. fin*. life history stages, thus for capelin, survival through the critical first-feeding stages may reflect the extent to which spawning time co-varies with abundance of this prey. Overall, with about a 2-2.5 month intermediary period between peak times of the two processes persisting each year since collapse, capelin have been about a month out of phase with their historical 'match' to the

bloom when a 1-1.5 month lag time was common. Theoretically, a closer match could be achieved either by earlier spawning or delayed blooms, but earlier spawning appears the more likely means by which early life stage capelin can exploit what appears to be the more optimal zooplankton prey community.

It is noteworthy that the window of opportunity for prime feeding conditions following the spring bloom is small. Initial stages of larval capelin growth are positively associated with the biomass of <250 *u*m zooplankton (Frank and Leggett, 1982a), which is represented by *C. fin.* at about the Nauplius III stage. This stage can be achieved in about three days post-hatching under virtually all environmental conditions (Campbell et al., 2001). Growth rates to larger stages are associated with phytoplankton community composition and temperature conditions (Diel and Breteler, 1986), but *C. fin.* can reach sizes equivalent to about stage IV in as little as 16 days under favourable conditions or as long as 45 days under unfavourable conditions (Campbell et al., 2001). In essence, when food is available, young capelin must capitalize.

4.5.2 Interactions of Key Processes

The analyses presented in this study demonstrate connectivity and pathways of effects from the base energy production stage of the NL shelf ecosystem to the success of its key energy conduit, capelin. Our results confirm the importance of sea ice dynamics on capelin year class strength (Buren et al., 2014), and provide a plausible mechanism through the match-mismatch of larval feeding with prey abundance. More generally, our results confirm that bottom up processes such as temperature and food availability are highly influential in regulating capelin success (Leggett et al.,1984; Frank and Leggett, 1981a;b; 1982a;b). The two factors of the

match-mismatch increment and the abundance of *CI-IV* account for much of the variation in capelin year-class strength.

Our study suggests warm, low-ice conditions are favourable for production of critical *CI-IV* copepods and in turn young capelin survival. Yet, we can not dismiss the possibility that the unexpected increase in abundance of historically 'cold state' zooplankton such as *Oithona* spp. are what is supporting recent increases in capelin abundance. Nonetheless, if current trends toward high levels of total zooplankton abundance and a decreasing lag time between spring bloom and capelin spawning continue, it would be anticipated that productivity in the northern capelin stock will continue to increase. The next few years could be particularly telling, with long cold winters, heavy ice conditions, and increased volumes of cold water occurring along the Newfoundland shelf in 2014 and 2015 (personal communication, Eugene Colbourne, DFO), which could theoretically stall the building momentum in stock recovery. However, assuming the relationship between age 0 and age 2 abundance continues to hold, our model predicts little change in age 2 capelin abundance during 2015.

4.6 Conclusions

Several key themes on the interactions of biophysical processes affecting capelin year-class strength arise from the analysis. First, sea ice is an important climatic driver of capelin productivity; second, the abundance of *CI-IV* (and by extension *Para-pseudocalanus*) copepods is critical to capelin success in this ecosystem; third, the match-mismatch of capelin spawning and the spring bloom is a key factor regulating year class strength, and, finally, warm temperate

conditions appear overall most favourable for stock productivity. Increases in capelin productivity in recent years have been associated with warming conditions, reduced ice coverage and earlier blooms, a declining trend in the mismatch with the spring bloom, and increases in both preferable and overall zooplankton abundance. Overall, it is apparent that processes operating in the climate system and at low trophic levels of the food-web act in concert to affect northern capelin and ultimately upper trophic level productivity in this ecosystem. Of these processes, the match-mismatch of spawning with the spring bloom and the abundance of *CI*-*IV* copepods are especially critical.

4.7 Acknowledgements

Nearly all data used in this study were provided from people and organizations outside the immediate realm of associates. Ice index data were provided by Alejandro Buren of DFO in St. John's, whom is thanked for both data and helpful discussions while this manuscript was being developed. Similarly, Fran Mowbray and other personnel from the Pelagics Section of DFO in St. John's require thanks for data on capelin spawning times and abundance estimates along with helpful discussions while the paper was being constructed. The Oceanography Section of DFO at the Bedford Institute of Oceanography in Dartmouth Nova Scotia is thanked for provision of Petrie Box temperature and Continuous Plankton Recorder data. Further, the efforts and helpful discussions of Eugene Colbourne and other colleagues from the Oceanography Section of DFO in St. John's are much appreciated. Finally, appreciation is expressed Timothée Govare for allowing insight into preliminary results from his Masters Program studies and helping provide evidence to bridge a key point in this paper.

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4.9 Figures

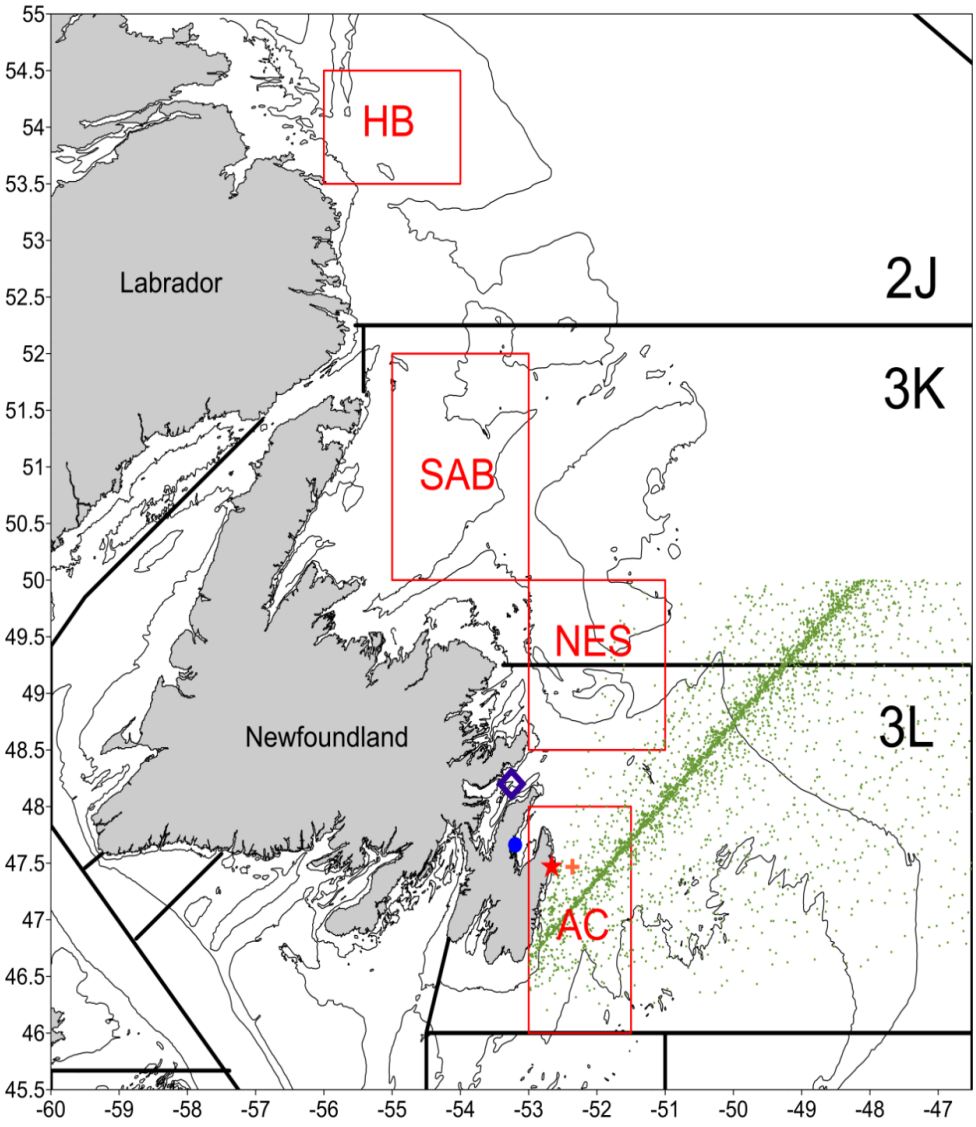

Figure 4.1. Map of the Newfoundland and Labrador Shelf showing features described in text. NAFO Divisions shown in black and Petrie Boxes shown in red (Hamilton Bank, St. Anthony Basin, Northeast Newfoundland Shelf, Avalon Channel). Blue circle shows location of Bryant's Cove, red star shows location of St. John's, orange cross shows location of Station 27, and purple diamond shows outer Trinity Bay. Green dots show locations of sample collections from the Continuous Plankton Recorder.

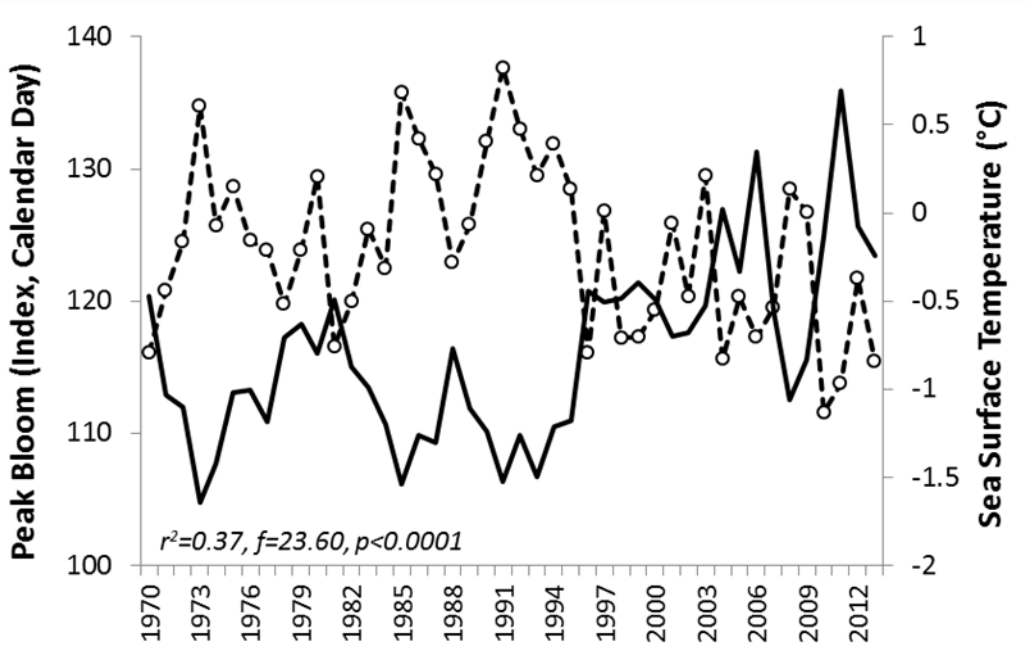

Figure 4.2. Proxy model of timing of the spring bloom (dashed line, open circles) in relation to January-April water column temperatures from Station 27 (solid line).

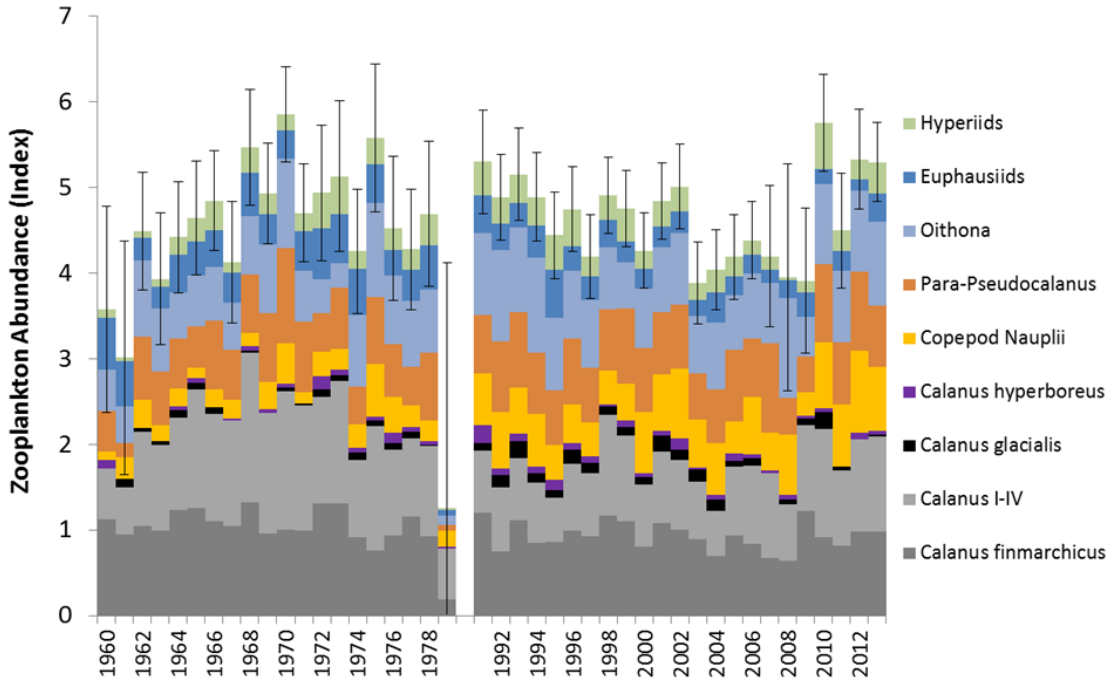

Figure 4.3. Least Squares Means estimates of dominant zooplankton taxa from the Continuous Plankton Recorder in NAFO Divisions 3KL. Error bars represent 2 standard errors for all taxa combined. Note data gap between 1979-1991.

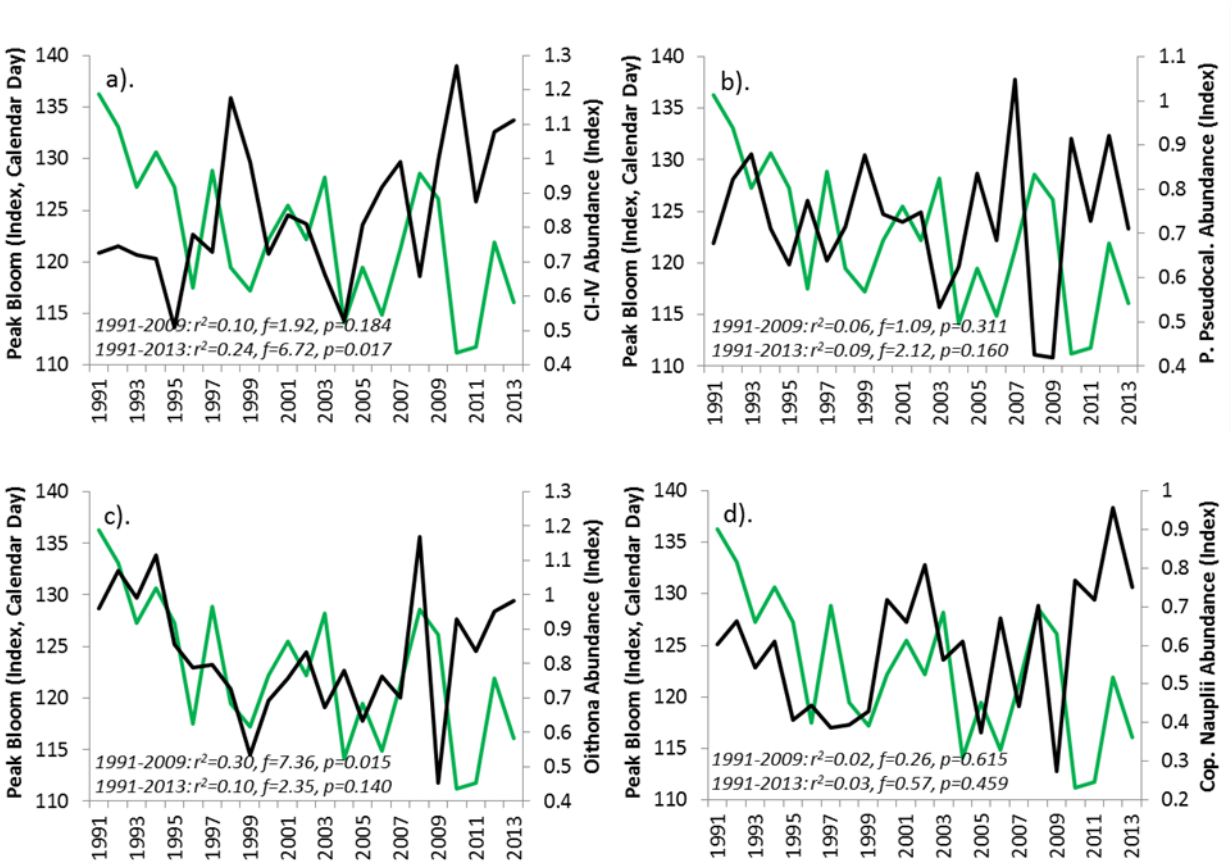

Figure 4.4. Peak spring bloom timing index (green line) versus abundance indices of key zooplankton taxa from the Continuous Plankton Recorder (black line); a). *Calanus I-IV*, b). *Para-pseudocalanus*, c). *Oithona* spp., d). Copepod Nauplii).

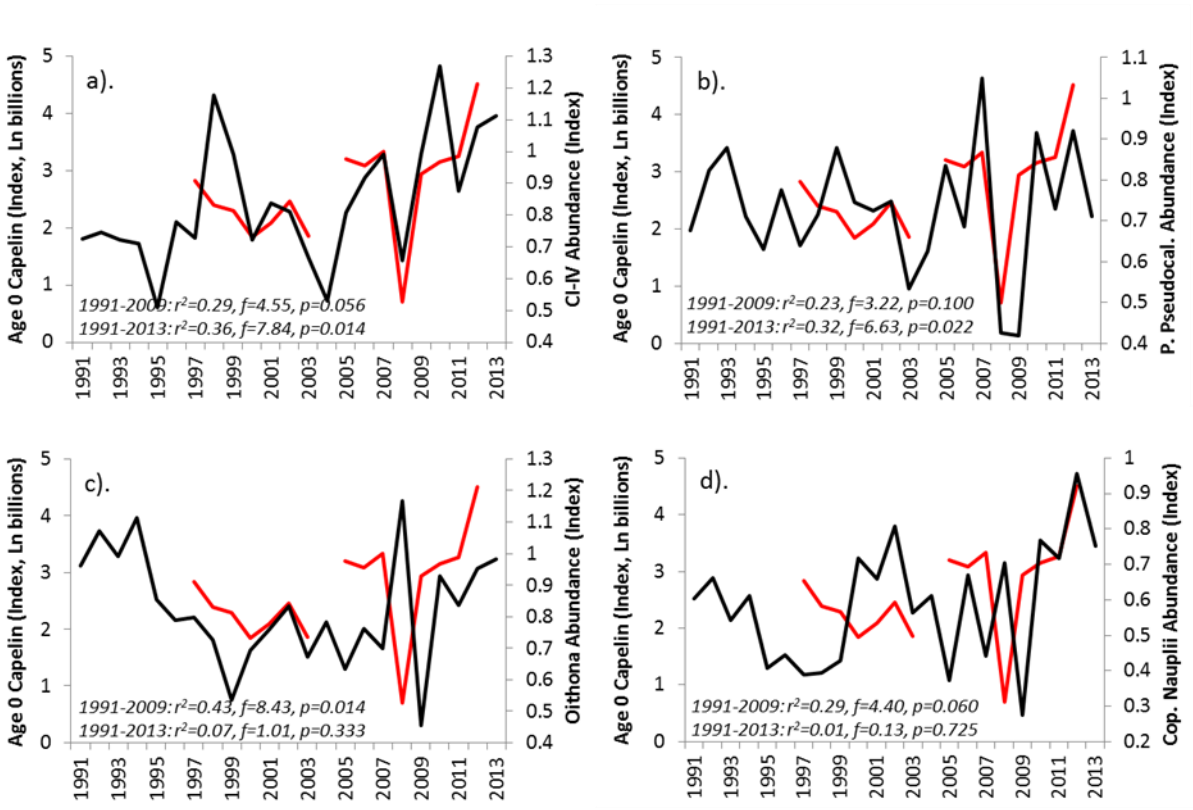

Figure 4.5. Age 0 capelin abundance index (red line) versus abundance indices of key zooplankton taxa from the Continuous Plankton Recorder (black line); a). *Calanus I-IV*, b). *Para-pseudocalanus*, c). *Oithona* spp., d). Copepod Nauplii).

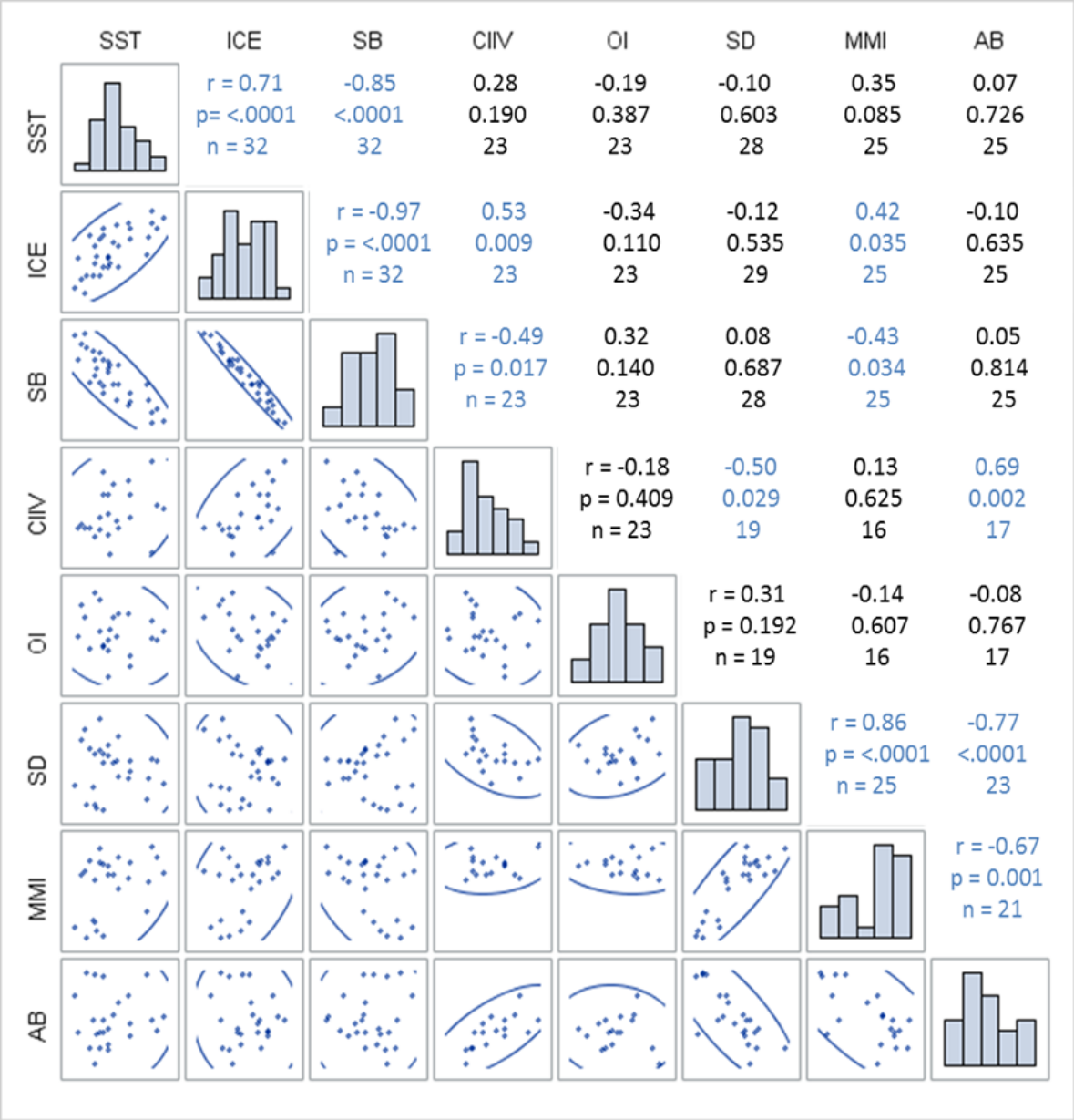

Figure 4.6. Scatter plot matrix of Jan.-Apr. sea surface temperature (SST) from the Northeast Shelf Petrie Box, the annual extent of sea ice (ICE), the peak timing of the spring bloom index (SB), the abundance of *CI-IV* (CIIV), the abundance of *Oithona spp.* (OI)), peak capelin spawning day (SD), the match-mismatch index (MMI), and capelin year-class strength (AB). Histograms are distributions of individual variables while ellipses are 95% probability predictors for each relationship. Pearson correlations shown with those significant at p<0.05 shaded in blue.

Figure 4.7. The Match-Mismatch index (open circles, dashed line) versus the abundance of age 0 capelin (solid line).

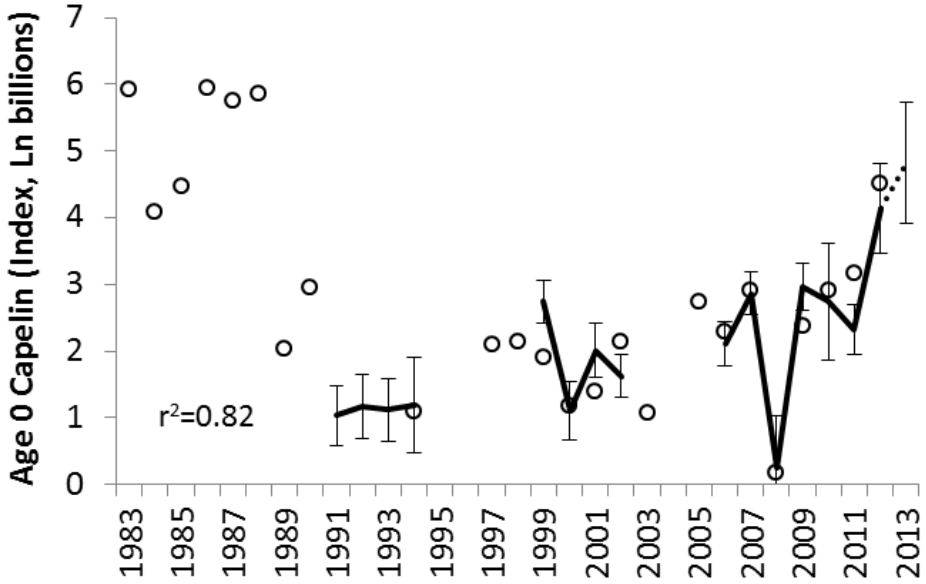

Figure 4.8. Point estimates of natural-log (Ln) abundance of age 0 capelin from acoustic surveys in NAFO Divisions 3KL (open circles) versus generalized liner model estimates and upper and lower 95% confidence intervals (Black line). Dashed line shows 2013 predicted value.

4.10 Tables

Table 4.1. Schedule of data availability for datasets used in the analysis. Black depicts years when data were available and white depicts omissions. See text for index-specific details. CPR refers to Continuous Plankton Recorder. For capelin, 'Spawn' refers to years when peak spawning day was estimated from beach surveys and 'Ab.' refers to years when abundance estimates were available from offshore acoustic surveys.

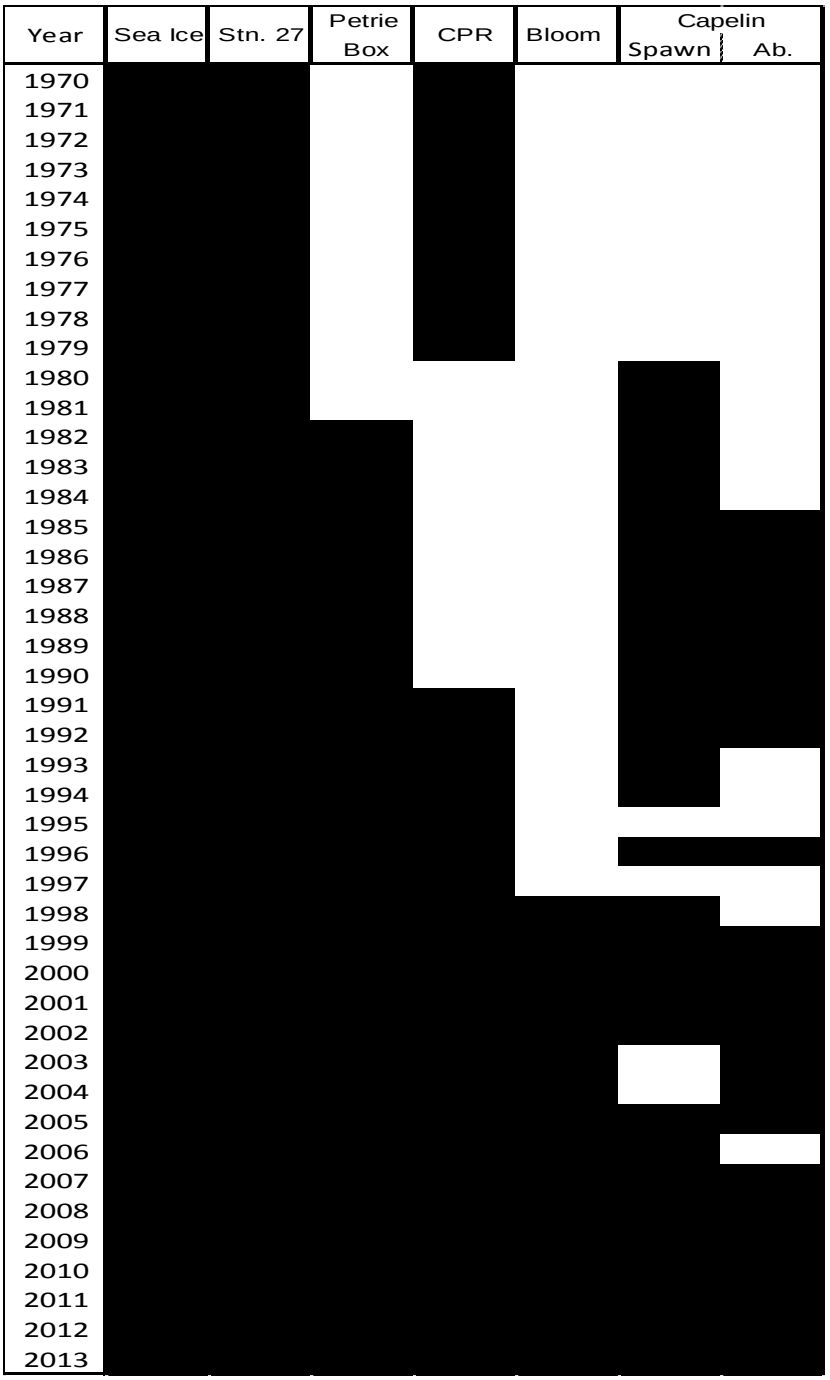

Table 4.2. Pearson correlation coefficients of satellite observations of spring bloom dynamics versus sea ice and surface temperature indices along the northeast Newfoundland Shelf from 1998-2010.

	Ice Latitude	Ice Area	Ice Retreat	SST
Bloom Start	-0.30	0.08	0.46	-0.30
Bloom Peak	-0.62	0.50	0.62	-0.57
Bloom Duration	-0.24	0.45	-0.02	-0.19
Bloom *chla*	0.67	-0.55	-0.39	0.25
Bloom Amplitude	0.31	-0.29	-0.28	0.18
Bloom Magnitude	0.05	0.20	-0.43	0.06

Table 4.3. Linear regression models of peak bloom timing versus sea ice and surface temperature indices along the northeast Newfoundland Shelf.

model	equation	r^2	*f*	*p*
peak bloom = ice extent (1998-2010)	y = -4.6458x + 339.02	0.39	6.91	0.023
peak bloom = ice area (1998-2010)	y = 0.0925x + 100.03	0.25	3.75	0.079
peak bloom = ice retreat date (1998-2010)	y = 0.2732x + 98.773	0.38	6.80	0.024
peak bloom = SST (1998-2010)	y = -17.317x + 103.29	0.32	5.29	0.042
peak bloom = ice extent (1998-2013)	y = -3.6896x + 294.37	0.28	5.46	0.035

Table 4.4. Output of generalized linear model. The model incorporated natural log of abundance of age 0 capelin as the response variable and the abundance of stage I-IV calanus copepds (CI-IV) and the Match Mismatch Index (MMI) and explanatory variables.

Analysis Of Maximum Likelihood Parameter Estimates							
Parameter	**DF**	**Estimate**	**Standard Error**	**95% Confidence Limits**		**Wald Chi-Square**	**Pr > Chi Sq**
Intercept	1	-30.054	8.8589	-48.9039	-11.204	11.51	0.0007
CIIV	1	41.0472	9.8641	20.0584	62.0361	17.32	<.0001
MMI	1	0.3713	0.1213	0.1132	0.6295	9.37	0.0022
CIIV*MMI	1	-0.4854	0.1338	-0.7701	-0.2008	13.17	0.0003
Scale	1	0.4693	0.0958	0.3297	0.7443		

Chapter 5

A review of factors contributing to the decline of Newfoundland and Labrador snow crab (Chionoecetes opilio)

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Chapter 5 focuses on evaluating factors contributing to the decline of snow crab in Newfoundland and Labrador. It qualitatively reviews an extensive body of research undertaken on NL snow crab in recent years, the majority of which I have led or been involved in. The finding that warming temperature is the most consistent cause of the decline across broad spatial and temporal scales follows the previous research chapters of this thesis in broadening the picture of how climate affects a host of resources in this ecosystem. Unlike the previous focal species cod and capelin, the impacts of warming are overall negative for this species, demonstrating how climate changes and trophic shifts create 'winners and losers' in the ecosystem. Chronologically and thematically, the chapter closes the research chapters of the thesis by examining how the present mainstay fishery will be impacted by ecosystem changes. Intuitively, at this point one might question where the ecosystem is heading next. Accordingly, this chapter suitably precedes the final synthesis and context chapter.

5.1 Abstract

The Newfoundland and Labrador snow crab resource, presently the basis of the most important commercial fishery in the region, is in decline. Short-, mid-, and long-term recruitment prospects are deemed poor in most areas. Fishery declines have been most apparent in the north, beginning in the mid- to late-2000s, but are expected to begin in the more productive southern areas in the near future. A multitude of emergent theories to explain the resource decline have been hypothesized as contributing factors, including overfishing, trawling impacts, seismic activities, disease, predation, and increasing temperature. This study comprehensively reviews and qualitatively relates the results of recent research and literature on each of these factors. Findings suggest several factors may be contributing to a lack of recruitment in the stock, but diminishing productivity resulting from a warming oceanographic regime is the primary cause of the resource decline. Further, it is postulated that trends occurring in the snow crab stock are indicative of a broader-scale ecological regime shift occurring along the Newfoundland and Labrador shelf.

5.1.1 Keywords: snow crab, Newfoundland and Labrador, regime shift, Atlantic multidecadal oscillation

5.2 Introduction

From the mid-1980s to early 1990s many fished and non-fished pelagic and groundfish species declined in abundance and exhibited shifts in distribution in the waters of the Northwest Atlantic off Newfoundland and Labrador (NL). On July 2, 1992, the Canadian Government imposed a fishery moratorium on the rapidly declining and formerly dominant "northern" Atlantic cod (*Gadus morhua*) stock off the northeast coast of Newfoundland and southern Labrador (Rose, 2007). Within a year all cod stocks in the region, along with other important fish stocks such as American Plaice (*Hippoglossoides platessoides*), were under similar closures. These events constituted the most significant event in the history of these fisheries, which had served as the socio-economic mainstay of the region since the early 1500s. The 30,000 workers displaced by the moratorium constituted the single largest mass lay-off in Canadian history. It appeared that after nearly 500 years the primary industry of the Northwest Atlantic, the fishery, was about to end. However, largely unknown to science, industry, and the general public, two species with much higher commercial value was rapidly increasing in these same waters and the fishery was on the verge of transition to one based primarily on 'crab' (Snow Crab - C*hionoecetes opilio*) and 'shrimp' (Northern Shrimp – *Pandalus borealis*).

Since the mid-1990s, the NL shelf has supported the world's largest snow crab fishery (Mullowney and Dawe, 2009). Although initial abundance levels are uncertain, it is certain that the stock and fishery grew rapidly following a cooling phase and collapse of finfish stocks in the late 1980s and early 1990s (see Figure 3 in Dawe et al., 2012a). Participation and value peaked in the mid-2000s, with over 3,500 active licences and landed values exceeding $300 million per

year (DFO unpublished data). However, after 2 decades of prosperity, the NL snow crab industry is now in decline, with recently contracting levels of activity in both the harvesting and processing sectors. In recent years, several hundred licence holders have exited the fishery and 7 of the 44 crab processing plants have closed. At the root of the industry decline is a resource decline. The resource and industry declines have been most apparent in northern areas (i.e. Northwest Atlantic Fisheries Organization (NAFO) Divisions 2HJ3K, Figure 5.1), beginning in the mid-late 2000s, but recent survey data suggest an imminent decline in the more productive southern areas (i.e. Divisions 3LNOPs), where the scale of prosecution is much higher (Mullowney et al., 2013). The impacts of a widespread downturn in the crab fishery may parallel the collapse of the cod fishery, with potential far-reaching socio-economic ramifications.

As with the collapse of the cod stocks, many hypotheses have been advanced by science and industry as causes for the decline in snow crab. Foremost among them are overfishing, trawling impacts, seismic activities, disease, predation, and increasing water temperatures. This study reviews literature on these diverse hypotheses, both in NL and other areas where snow crab occurs, in an attempt to better understand and predict the future state of the ecosystem, its community composition, and the likely impacts on the fishery. The objective of this paper is to qualitatively review, synthesize, and apply these recent findings to broad-scale trends occurring in the Newfoundland and Labrador snow crab resource.

5.3 Snow Crab Biology and Management

The snow crab is a stenothermal sub-arctic species inhabiting cold waters of about -1.5° to 4°C (Dawe and Colbourne, 2002; Dawe et al., 2012b). The species is sexually dimorphic with males achieving larger sizes than females. Maximum size in Atlantic Canada is about 95 mm carapace width (CW) for females and 150 mm CW for males (Sainte-Marie and Hazel, 1992; Sainte-Marie et al., 1995). To help maintain reproductive potential, fishery regulations prohibit the retention of all females and males under 95 mm CW. Growth is a stepwise process associated with molting, which ceases after a terminal molt (Conan and Comeau, 1986). This can occur at sizes as small as 30 or 40 mm CW for females and males respectively. Molt frequency is highest during early ontogeny but slows to a near-annual occurrence at larger sizes (Sainte-Marie et al., 1996).

Mating and molting normally occurs during spring, but first-time mating (primiparous) females can occur during winter. For females, the terminal molt into adulthood is the puberty molt, but for males the puberty molt occurs before the terminal molt, with male crabs being sexually mature adolescents for a variable number of years before terminally molting into adulthood. Following a molt, crabs are in a soft-shelled condition and it can take up to a year for shells to harden and meat content to progress to a commercially acceptable level. During terminal molt males develop enlarged chela, a trait likely beneficial in competition for food or mates. Maximum longevity following terminal molt is about 7 to 8 years (Fonseca and Sainte-Marie, 2008). Bottom temperature relates negatively to abundance (Marcello et al., 2012) and positively to size (Dawe et al., 2012b). Snow crab appear to follow a fitness strategy of

settlement in shallow cold areas to maximize early-life survival followed by ontogenetic migrations to deep warm areas to maximize size. The fishery focuses primarily upon deep areas in bays and between offshore banks where large males are most commonly distributed (Dawe and Colbourne, 2002).

Much of the management focus for snow crab is on minimizing the capture of soft-shell crabs, which are commercially undesirable and represent future recruitment to the fishery. Mortality associated with capturing and releasing soft-shell crabs is unknown but thought to be high (Mullowney et al., 2012; 2013). Historically, the fishery was prosecuted during the summer and fall, but in recent years it has shifted to spring and early summer to minimize the capture of soft-shell crabs, which become increasingly mobile over the summer as shells harden.

The stock assessment for snow crab in NL is conducted annually, during late winter, with quotas subsequently allocated for the spring fishery within 44 small-scale management areas. The minimum required mesh size in the pots is 5.25" (133 mm), intended to allow the escapement of under-sized male and all female crabs, but 5.5" (140 mm) gear has become increasingly commonplace in the fishery. Other pertinent management measures include mandatory observer coverage (about 5 %) for all fleet sectors, the use of vessel monitoring systems (VMS) in offshore fleet sectors, mandatory completion of logbooks, a dockside monitoring program for landings, and a soft-shell protocol whereby fishing grids are closed for the duration of the season when soft-shell crabs constitute 15 % (Divisions 3LNO) or 20 % (Divisions 2HJ3KPs4R) of the observed catch.

5.4 Resource Status

The stock assessments incorporate a variety of fishery dependent and independent information (Mullowney et al., 2013). A depth-stratified random trawl survey occurring each fall in NAFO Divisions 2HJ3KLNO (Figure 5.1) forms the primary basis for estimation of exploitable and pre-recruit biomass indices and advice. Biomass estimates are derived from swept area extrapolation of catch rates to depth-based strata that cover most of the NL Shelf (Smith and Somerton, 1981; and see Mullowney et al., 2013 for further details). The exploitable biomass of crabs comprises adult males ≥95 mm CW, while pre-recruits are adolescent males ≥76 mm CW, which are deemed capable of achieving exploitable size following another molt. The capture efficiency of snow crab by the survey trawl is known to be low for all sizes of crab, but is most inefficient for smallest individuals and on hardest substrates (Dawe et al., 2010a). Accordingly, the exploitable and pre-recruit indices are known to be underestimates of true abundance and biomass. No stock-recruitment relationship is evident for this stock, which could reflect inefficient survey performance or intrinsic or extrinsic biological factors.

Overall, the exploitable and pre-recruit biomass indices are both currently in decline, after peaks in the late 1990s and between 2008 and 2010 (Figure 5.2). The latter peak was smaller than the earlier one, but improved management and fishing practices likely contributed to maximizing more of the resource potential, as fishery landings have been maintained at 50,000-60,000 t since 1999 (Mullowney et al., 2013). As quotas are allocated annually, much of the scientific and management focus tends to be centred on short-term recruitment prospects and available exploitable biomass. However, in recent years it has become increasingly apparent

that recruitment prospects are diminishing and more attention has been given to predicting long-term outcomes. The most recent stock assessments have concluded that short-, mid-, and long-term recruitment prospects are unfavourable across the entire NL shelf (Mullowney et al., 2013). Diminishing recruitment prospects are reflected in trawl survey size frequency distributions of males (Figure 5.3), which show reduced abundance of all sizes in recent years. Of particular concern is the paucity of small crabs (i.e. <50mm CW) in the survey since 2003. Furthermore, there has been a marked decrease in the abundance of mature females, to historical lows for the survey time series, in the past three years (Figure 5.4). Overall, the prognosis for the resource and fishery is reduced production and a smaller fishery in the coming decade.

The concerns of science and the fishing industry about what is occurring to cause or promote the decline of snow crab have elevated in recent years. Compared to the situation with cod in the late 1980s, there is more broadly accepted consensus that the resource is declining, but as with the cod collapse, the impact on the fishery is likely to have enormous ramifications. The subsequent sections highlight the results of recent research and qualitatively evaluate information on potential contributing factors.

5.5 Analysis

5.5.1 Fishing

Anthropogenically-driven top-down impacts from fishing are always a possibility when fishery resources go into decline. Fishing has the potential to directly impact both present and future

stock abundance and productivity, with the mechanisms of harm and full breadth of repercussions rarely understood. Impacts of severe overfishing can resonate long after fishing ceases. In the NL snow crab fishery, large mesh pots are used, thereby restricting the catch to large males. Hence, the probability of inflicting direct mortality or serious harm to females and small males is low, with sexual dimorphism in this species imputing some inherent resilience to fishing. The greatest concern for top-down fishery impacts is over-exploitation of large and pre-recruit-sized males.

It is possible that long-term productivity could be impacted by the removal of too many large males, although there is no known relationship between large male abundance and recruitment potential. Interestingly, however, recent work on red king crab (*Paralithodes camtschaticus*) in Norway found that the removal of high numbers of large males can lead to a coincidental reduction in the size of ovigorous females, either due to decreased post-molt protection from large males or increased rates of capture in the fishery, and that sperm limitation can become an issue when largest breeding males are removed (Hjelset et al., 2012; Hjelset, 2013). Nevertheless, there is no evidence of fecundity issues in NL snow crab, with >80% of mature females consistently carrying full clutches of viable eggs in all areas since 1995 (Mullowney et al., 2013). Long-term effects of fishery exploitation remain open to question.

In the short- to medium- terms the management of snow crab stocks typically aims to maintain production by protecting females and a portion of the largest adult males, as well as all small adult and adolescent males. This strategy relies on assumptions that females need only be mated once to produce several clutches of viable eggs with stored sperm (Sainte-Marie and

Hazel, 1992), and that strong recruitment has been evident in years with seemingly low abundance of large males. This could reflect differences in mating and fishery timing, with the spring-summer fishery occurring later than the mating period.

The trend in the exploitation rate index for Divisions 2HJ3KLNO, calculated as the ratio of landings to the exploitable biomass index from the previous survey, is inversely related to the trend in exploitable biomass (Figure 5.2). This indicates that landings have remained constant relative to fluctuations occurring in the exploitable biomass. The exploitation rate index was lowest in the late 1990s, highest in the early 2000s, at a secondary low in the late 2000s, and at a secondary high in the past three years.

The overall trends in the exploitable and pre-recruit biomass indices incorporate division-specific variability within them. There has been a general pattern of a spatiotemporal cline with events occurring first in the north and following in succession southward. For example, the most recent peaks in exploitable biomass occurred in Divisions 2HJ in 2006-2007, in Division 3K in 2007-2008, and in Divisions 3LNO and Subdivision 3Ps in 2009 (Mullowney et al., 2013). The fishery has exhibited a similar clinal pattern, with catch rates most recently peaking in Divisions 2HJ and 3K in 2007-2008 versus 2009 in Subdivision 3Ps. However, Divisions 3LNO have countered the trend, with increasing fishery catch rates in recent years. This is thought to reflect a lower level of exploitation in Divisions 3LNO compared to other Divisions and consequently a higher residual component to the exploitable biomass (i.e. less dependent upon immediate recruitment each year). This phenomenon largely accounts for the cessation of decline in the overall exploitable biomass index from 2011 to 2012 (Figure 5.2), with Divisions

3LNO most significantly weighting the data. However, of particular concern is that the declining trend in the pre-recruit biomass index has been increasingly weighted by Divisions 3LNO in the past two years, with declines in other Divisions beginning earlier.

Apart from the obvious effect of direct removals by fishing, the issue of greatest concern is the capture and release of soft-shell crabs, with incidence in the fishery reflecting both seasonality and large male density (Mullowney et al., 2012). Soft-shell prevalence normally increases throughout the summer, as crabs that molted in the spring become increasingly mobile, but becomes accelerated when the density of large hard-shelled males is reduced. This likely reflects an increased catchability of soft-shell crabs due to a decreased level of competition for baited pots. As such, high prevalence of soft-shell crabs can serve as a direct indicator of recruitment overfishing as it signifies a low density of large competitive males. A continuation of fishing activities during periods of high soft-shell prevalence has the potential to reduce the numbers of pre-recruits and consequently impact near-future fisheries. Soft-shell crab incidence, based on at-sea observer sampling throughout the year, is consistently highest in Division 2J, tends to be relatively high in Division 3K, is consistently very low in Divisions 3LNO, and arises only occasionally in Subdivision 3Ps (Figure 5.5). Overall, with the exception of a high catch rate in Division 2J in 2012, soft-shell crab catch rates have been lower in recent years relative to pre-2006 levels. This trend is consistent with the management shift toward earlier (spring) fisheries since the mid-2000s. The highest incidence consistently occurs in northern Divisions (2J3K), where the biomass is low relative to Divisions 3LNO (Mullowney et al., 2013), and is not consistent with soft-shell mortality being a primary driver of the overall declining trends in the broader-scale pre-recruit and exploitable biomass indices (Figure 5.2).

In summary, although fishing pressure is higher now than during the most recent resource peak it cannot be ascribed as the primary driver of broad-scale resource trends. The overall exploitation rate is moderate relative to historical levels, especially in the most important areas (i.e. 3LNO), and soft-shell crab prevalence in the catch is relatively low in recent years. It is possible that overfishing could be exacerbating the decline or prohibiting recovery in some areas (i.e. 2HJ3K), but it does not account for the broad-scale and prolonged decline occurring in the stock as a whole.

5.5.2 Shrimp Trawling

Other human activities occurring on the snow crab grounds have been postulated to have driven the crab decline in some areas. One such activity that has garnered considerable attention is shrimp trawling.

The northern shrimp fishery in NL waters occurs from the tip of Labrador in the north to the northern portion of the Grand Bank in the south (Figure 5.1; Orr and Sullivan, 2012). In general, much of the activity is concentrated on muddy substrates along the slope edges of the continental shelf, where crab fishing effort is minimal. However, in Divisions 2J3K where industry outcry has been particularly strong, about 18-32 % of the fishing grounds of the two fisheries may overlap in any given year (unpublished data). Schwinghamer et al. (1998) found no significant impacts of trawling on snow crab on the Grand Bank, but did note some dead crabs in the tow path of the trawl. Subsequently, two separate collaborative studies carried out by industry and both levels of government (i.e. Federal/Provincial) using secondary retainer

bags in the trawl as well as a Remotely Operated Vehicle (ROV) to observe trawl-induced damage and mortality concluded there is no significant impact of trawling on snow crab (FDP 2002; Dawe et al., 2007). The latter and more comprehensive study found no evidence of trawling-induced mortality or damage from post-trawl videos. Similarly, post-trawl trapping using both large- and small-mesh pots found no evidence of carapace damage or leg loss in crabs where trawling had occurred (Figure 5.6). Crab specimens captured in the trawl showed elevated levels of new carapace damage and leg loss (Figure 5.6), which was attributed to post-capture damage inside the trawl itself (Dawe et al., 2007).

Two large areas closed to trawling and other bottom impact fisheries were established during 2002-2005 as precautionary measures to protect snow crab from potential harm (Figure 5.1). The effectiveness of the larger and initially established Hawke Box in Division 2J was reviewed by Mullowney et al. (2012), who found that any potential positive outcomes from the cessation of trawling had been masked by excessive crab fishing activity following the closure. No formal studies have been done on the Funk Island Deep closure, but the most recent stock assessments suggest it has had a similar outcome (Mullowney et al. 2013). In both cases, pre-closure fishery catch rates of snow crab were generally higher inside the areas, relative to adjacent fishing grounds, but since closure catch rates have come together and shown no difference (Figure 5.7). Neither closure has been successful in protecting pre-recruit crabs from mortality because the crab fishery itself has imposed a higher level of mortality on the resource than shrimp trawling. These results, however, do not preclude the notion that productivity of

snow crab may have increased within the closed areas, with this aspect currently under investigation in an independent study (Rose, unpublished data).

The shrimp trawling fishery has the largest potential for by-catch of snow crab in the region, with pelagic and benthic hook and line fisheries not likely to capture high numbers of snow crab. Dawe et al. (2007) estimated bycatch in shrimp trawls to average 1-2 kg./tow and total removals by the large-vessel shrimp fleet, which receives 100% at-sea observer coverage, to total about 0.25-2 t per year. The removals by the small-vessel shrimp fleet are unknown, but with such low by-catch in the large vessel fishery there appears little cause for concern of any significant effect from direct removals of snow crab by shrimp boats.

Trawls with rockhopper footgear used in Newfoundland and Labrador, including for scientific surveys, are known to have low capture efficiencies for snow crab (Dawe et al., 2010a; Mullowney et al., 2013). Despite low capture efficiency, a recent study using video observations on the footrope of a bottom trawl demonstrated that about 50 % of large crabs experienced direct contact with the gear before passing beneath it (personal communication, Dr. Paul Winger, Marine Institute of Memorial University, St. John's, Canada), demonstrating the potential for interaction.

The evidence currently compiled does not suggest that shrimp trawling is the main factor driving recent snow crab resource declines. Although there is a potential for some mortality and damage, studies to date suggest it is relatively minor, with other factors such as crab fishing

itself exhibiting greater impacts. Nonetheless, the issue of shrimp trawling impacts on snow crab remains a contentious one in NL and further studies on the matter are on-going.

5.5.3 Seismic Activities

To date, potential impacts of seismic activities on snow crab have received only limited formal study, with few published papers on the topic. In a review on the effects of seismic and marine noise on invertebrates, Moryiasu et al. (2004) cautioned that because of the predominance of gray literature that general consensus conclusions of invertebrates being robust to seismic noise should be treated cautiously.

Christian et al. (2003) and DFO (2004) found no immediate or latent mortality or effects on a variety of haematological and histopathological parameters for snow crab exposed to seismic guns at distances of 2 to 4 m, but did suggest latent developmental effects could occur in larvae. Payne et al. (2007) found no immediate or delayed effects of damage or mortality to American Lobster (*Homarus americanus*) in lab and field experiments when Gulf of St. Lawrence lobsters were exposed to seismic noise. In a study directed at crab larvae, Pearson et al. (1994) exposed early stage Dungeness Crab (*Cancer magister*) to maximum sound levels encountered during seismic surveys, with the air gun as close a 1 m, and found no immediate or latent mortality. Similarly, preliminary results from tank-based observations of exposure to seismic noise on snow crab have suggested there is no impact on egg development or immediate or

latent mortality from episodic exposure to high sound levels (personal communication, Dr. Jerry Payne (DFO)).

The on-going work on snow crab is suggesting it is possible they become stressed from exposure to seismic noise, as interpreted from a drop in blood parameters following exposure. American Lobsters experienced similar stress following exposure, with a drop in serum enzymes, protein, and calcium, and changes in feeding behaviour (increased consumption). Wale et al. (2013) recently showed that noise from lower level sources such as ships altered behaviour in the shallow water European Shore Crab (*Cancer Maenus*) by disrupting feeding, slowing reaction time to threats, and hastening turn-over times for crabs placed on their backs. They inferred that such behavioural alterations could increase the susceptibility to starvation or predation in the wild.

In summary, the evidence compiled to date does not suggest that seismic activities have significantly contributed to recent snow crab resource declines. Although it is possible that seismic noise could induce physiological or behavioural changes in crabs, no studies to date have found any direct or latent damage or mortality from noise exposure. Any mortality associated with post-exposure physiological or behavioural alterations is theoretical and undemonstrated. Nonetheless, many crab harvesters remain concerned about seismic exploration along the NL shelf.

5.5.4 Disease

Disease-induced mortality may regulate a population. Along the NL shelf, the only known disease fatal to snow crab is Bitter Crab Disease (BCD). BCD is a hemo-parasitic affliction caused by infective dinoflagellates of the genus *Hematodinium*. The increased metabolic load stemming from infection normally results in respiratory and/or organ dysfunction and subsequent death. Parasitic transmission is typically associated with host molting (Eaton et al., 1991; Stentiford and Shields, 2005), thus in snow crab infection likely occurs during spring. Infected crabs may be identified visibly by fall and death likely occurs over winter. BCD prevalence has been monitored by macroscopic analyses from the fall multi-species trawl surveys since 1995. These macroscopic diagnostics are known to underestimate true prevalence (Dawe et al., 2010b; Mullowney et al., 2011), but an ongoing study has confirmed trends are consistent with those determined through more sensitive polymerase chain reaction DNA sequencing (unpublished data).

Dawe et al. (2010b) reported that ocean circulation features and host population dynamics influenced distribution of BCD along the NL shelf. The highest infection rates were typically associated with shallow areas, such as the top of offshore banks, where small crabs are most common (Dawe and Colbourne, 2002). Shields et al. (2005, 2007) studied BCD prevalence and distribution dynamics in snow crab from Conception Bay in inshore Division 3L, and concluded that the disease was positively related to ocean temperature. They predicted future warming would lead to increased prevalence and distribution, and consequently elevated natural mortality levels in NL snow crab. However, counter to this, as the ocean climate along the NL

shelf has warmed since the mid-1990s (Colbourne et al., 2012) overall BCD prevalence levels have decreased (Mullowney et al., 2013).

Mullowney et al. (2011) studied BCD in snow crab from bays in Division 3K and found no direct relationship with ocean temperature. In contrast, they found the disease was density regulated, with infection rates reflecting the relative abundance of small and intermediate-sized crabs. The disease was deemed to alter populations most during periods of high recruitment. Moreover, they found that BCD prevalence levels could be used as an index of long-term recruitment potential for the fishery. The relationship with temperature was found to be indirect, with temperature regulating small crab abundance, which in turn largely determined overall disease prevalence. Accordingly, as the relationship between temperature and small crab abundance is negative, they argued that reduced BCD prevalence and subsequent mortality in the snow crab would be expected as ocean temperatures increased.

The two groups of male crabs most commonly infected are new-shelled adolescents ranging 40-59 and 60-75 mm CW (Mullowney et al., 2013). An examination of annual trends in these groups shows that the prevalence of BCD has indeed decreased in recent years (Figure 5.8). In Division 2J, prevalence was exceptionally high in 1999 and has been low since, while in Division 3K there has been a gradual decline in annual prevalence levels since 1997. The 2010 observations in Division 3K were deemed anomalous due to mis-classification (Mullowney et al., 2013). In Divisions 3LNO, an increase during the 2003-2005 period reflected the progression of a recruitment pulse through those sizes, which has subsequently progressed into

the exploitable biomass and become manifest in recent high fishery catch rates (Mullowney et al., 2013).

In summary, the overall decreased prevalence of BCD in recent years indicates that mortality from this disease is not the primary driver of recent declines in the crab resource. However, a broad-scale reduction in BCD is consistent with other data in suggesting a low level of production and recruitment.

5.5.5 Predation

Along the NL shelf, the historically dominant predator in the ecosystem was Atlantic cod (*Gadus morhua*). Other predators with the potential to influence snow crab abundance include wolffishes (northern (*Anarhichas denticulatus*), spotted (*A. minor*), and Atlantic (*A. lupus*)), Greenland halibut (*Reinhardtius hippoglossoides*), thorny skate (*Amblyraja radiate*), and harp seals (*Pagophilus groenlandicus*).

The cod stocks surrounding Newfoundland and southern Labrador (Divisions 2J3KL) were once among the world's largest (Rose, 2007). However, during the late 1980s and early 1990s they collapsed, along with most of the finfish community, leading to the commercial fishing moratoria. Concomitant decreases in size- and age-at maturity and condition were associated with high levels of natural mortality during and subsequent to the collapse. However, some recovery has occurred in recent years (Rose et al., 2011), and some crab harvesters claim that cod is now exerting top-down control and contributing to the decline of the resource. Based on a meta-analysis of cod and crab correlation coefficients, Boudreau et al. (2011) concluded that

cod predation can exert a top-down regulating influence on large juvenile and sub-adult snow crab, lending support to the observations of some crab harvesters that increasing numbers of cod are causing declines in crab.

Any discussion of cod predation on snow crab must consider that impacts will be lagged in the fishery or exploitable biomass by several years because cod gape limitations render small crabs most susceptible to consumption and largest crabs virtually immune. For example, Chabot et al. (2008) demonstrated that nearly all consumed crabs were less than about 40 mm CW. Large cod of about 80 cm total length (FL) or more are able to consume an intermediate-sized crab of about 65 mm CW. Dawe et al. (2012a) showed only marginal consumption of crab by cod for the past two decades (Figure 5.9), but the study did not include data after 2009 and during the time of the study few large cod were present in the major crab grounds (Brattey et al., 2010). A study incorporating cod diet data up to 2011 when larger fish were present also reported few snow crabs in the stomach contents from various stocks in NL waters (Krumsick and Rose, 2012). Hence, the general absence of large cod in the previous decades and the lack of crab in more recent cod diet studies of primarily smaller cod suggests that predation by cod is not broad-based and any regulating effect on snow crab recruitment or adult mortality is likely to be minor. It is noteworthy, nonetheless, that recent increases in the abundance of large cod in some areas (i.e. Division 3K) (Rose, unpublished data) may have elevated the potential for cod to impact some crab groups.

The weight of the evidence suggests that cod predation is not responsible for the presently observed recruitment declines or adult mortality in snow crab. This is not to say that predation

could not reduce crab populations, but until recently the abundance of large (i.e. age 5+) cod has been near-universally too low in the NL ecosystems to have significant impact. Nonetheless, the increasing numbers of larger cod in some areas could exacerbate rates of decline. Indeed, recently increased predation could partially explain the increased rate of decline in mature female crab abundance in the past three years (Figure 5.4). In the Eastern Bering Sea, Orensanz et al. (2004) described a situation whereby cod predation was prohibiting female snow crab from re-establishing their distributional range to the south, following a climate-induced northward contraction, providing evidence of the potential for cod to impact snow crab stocks.

Other finfish species might also prey on snow crab and influence their numbers. Greenland halibut abundance along the NL shelf did not decline as precipitously as most other predatory finfish species during the late 1980s and early 1990s, and this species maintained a higher potential to regulate crab than most other top predators. However, the diet of Greenland halibut has been highly piscivorous since the late 1970s, with little consumption of snow crab (Dwyer et al., 2010; Dawe et al., 2012b).

Thorny skate and wolffishes might also feed on snow crab, but long-term population abundance has likely been too low for these species to account for long-term declines in snow crab. These species' have been reviewed by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) in recent years (Simpson et al., 2011; 2012), with northern and spotted wolfish deemed threatened and Atlantic wolfish and thorny skate of special concern. Moreover, the diet of thorny skate in the Northwest Atlantic is varied, consisting mainly of

small pelagic fishes, crabs (including snow crab), cephalopods, polychaetes, and amphipods (Templeman, 1982). There is limited information available on the diet of wolffishes along the NL shelf, but some on-going work has shown it to be highly varied with no single species dominating and low consumption of snow crab (Simpson et al., 2013).

The abundance of harp seals along the NL shelf has steadily increased since the early 1970s and has sustained itself near a historical high since the mid-1990s (Stenson et al., 2009). This species may have been the top predator exerting top-down influence in the NL shelf ecosystem since the collapse of cod (Lilly et al., 2008; Bundy et al., 2009). There have been increased accounts by fish harvesters in some northern areas in recent years of seeing snow crab on the surface ice during winter and spring, which has been attributed to seal predation. However, analyses of the offshore diet of harp seals has shown virtually no snow crab consumption during winter and summer sampling since the mid-1980s (Stenson et al., 2009).

In summary, predation by cod is unlikely to account for long-term and broad-scale declines that have occurred in snow crab. Nevertheless, recent increases in large cod may increase predation and exacerbate the rate of crab decline. There is little evidence that Greenland halibut or harp seals have any regulating effect on snow crab.

5.5.6 Ocean Climate

Zoogeographic evidence shows that snow crab is restricted to sub-arctic ecosystems where cold water persists. Three recent independent studies using data on the two variables with sufficient time series (temperature, predator abundance) for modeling from our region have reported similar results, with temperature key to distribution and abundance of snow crab.

First, Boudreau et al. (2011) concluded, based on an Atlantic Canadian-wide meta-analysis of correlation coefficients of crab, cod, and temperature, that temperature exerts a bottom-up influence on small crab with cold conditions favourable. Subsequently, in a multivariate regression analysis Marcello et al. (2012) compared the effects of temperature in relation to cod predation and crab spawning stock biomass on crab recruitment along the NL shelf, in the southern Gulf of St. Lawrence, and in the Eastern Bering Sea. They found that cold ocean conditions during early ontogeny was the only factor consistently associated with strong recruitment. Finally, in a multi-species study on the NL Shelf using geographic weighted regressions, Windle et al. (2012) found that snow crab abundance was better predicted by environmental variables (i.e. temperature) than predator abundance.

The effect of cold bottom temperature on future fisheries is evident from the negative relationship of data from Station 27, adjacent to the Grand Bank, to future catch per unit of effort (CPUE) in Divisions 3LNO at a lag of 9 years (*f=11.75, p=0.002*). Similarly, a strong positive ($p<0.0001$) relationship occurs between CPUE and habitat index (areal extent of <1 °C bottom water) at a lag of 10 years (Figure 5.10). We chose to present the relationship of CPUE against Station 27 temperature because it is the longest and most consistently sampled oceanographic monitoring site in Northwest Atlantic, and provides the only satisfactorily long time series for cross-correlation when lags necessary to project back from 'fishery-size' to smallest sizes of crabs are applied (i.e. 9-10 years). Similar relationships of CPUE, as well as exploitable biomass, with lagged bottom temperature and habitat indices occur in all areas of the NL Shelf (i.e. Div. 2J3KLNOP4R), albeit with shorter time series (Mullowney et al., 2013). Furthermore, the lags are longer in coldest areas, such as Divisions 3LNO, due to a lower molt frequency (higher

incidence of skip-molting) in cold conditions (Dawe et al., 2012a) and perhaps a longer period of egg retention in cold (i.e. two years) versus warm (i.e. one year) areas (Mallet et al., 1993; Sainte-Marie et al., 1993).

Relationships between the environment and future fisheries only indirectly address the effects on early-life survival of small crabs. Nevertheless, their consistency across all areas of the NL shelf strongly suggests that thermal mechanisms influence early-life survival. Where survey data allowed, Marcello et al. (2012) more directly addressed the impact of temperature on recruitment in other areas (i.e. Eastern Bering Sea, Southern Gulf of St. Lawrence), similarly finding strong, negative, and consistent relationships between bottom temperature and early-life survival. To test and validate the relationship in NL waters, they used lagged CPUE as a proxy for recruitment due to concerns with the short times series of survey data and poor catchability of snow crab by the Campelen trawl.

The strength of the argument for a strong direct effect of temperature on early-life survival lies in the consistency seen among major snow crab stocks on a global scale, including different areas of the NL shelf operating under different temperature regimes ('warm' Divisions 2J3K vs. 'cold' Divisions 3LNOPs). Based upon this recently advanced knowledge, stock assessments in NL have included a long-term projection based on thermal habitat indices in each Division (Mullowney et al., 2013). To explicitly focus the temperature analysis on smallest crabs, the division-specific indices are restricted to shallow (i.e. ≤200 m) areas, corresponding tightly with distribution of smallest crabs, which are rarely observed in deep areas (Dawe and Colbourne, 2002). Although cold water dominates this small crab habitat, crabs migrate to deeper, warmer

areas over the course of life (Dawe and Colbourne, 2002; Mullowney et al., 2011). The stratification of the water column, with shallow areas coldest, is a function of the distribution of the cold intermediate layer (CIL), a body of cold water (<0°C) intermediate in the water column resulting from winter cooling. In the deep northern areas (Divisions 2J3K) there is limited distribution of shallow or <1°C bottom water and the habitat indices are more loosely defined as bottom water <2°C from shallowest areas (i.e. ≤300 m).

An examination of smoothed third-order polynomial regression models of the habitat indices for each Division (Figure 5.11) shows a clear contraction of the cold water mass across the entire NL shelf since the early 1990s, with expansion to peak levels occurring in the late 1980s in northern Divisions 2J3K and the early 1990s in southern Divisions 3LNOPs. The growth of the cold water mass throughout the 1980s resulted in a highly productive period for the stock that led to unprecedented levels of exploitable biomass in the mid- to late-1990s (Figure 5.2). Accordingly, with reductions in cold bottom water occurring across the entire NL shelf for the past two decades, with some Division-specific variability, the long-term outlook for snow crab is unfavourable across the entire NL shelf (Mullowney et al., 2013).

Apart from driving production and recruitment potential, temperature also impacts stock biomass via a direct effect on crab size. Dawe et al. (2012b) showed that size-at-terminal molt is positively related to prevailing thermal conditions, with crabs in warm regions consistently achieving greater sizes than crabs in cold regions. In NL, the deeper and warmer northern areas of the continental shelf (i.e. Divisions 2HJ3K) house crabs that achieve larger sizes on average. However, cold areas are more productive and able to support larger-scale fisheries. Overall,

the negative effects of warm conditions on productivity and recruitment are greater than the positive effects on individual size in regulating overall stock biomass (Dawe et al. 2012b).

In summary, a recently warming oceanographic regime is fully consistent with the prolonged and broad-scale decline in productivity and recruitment in NL snow crab.

5.6 Discussion

5.6.1 Summary

A prolonged period of low productivity and recruitment has resulted in declines in all components of the Newfoundland and Labrador snow crab resource over the past decade. This is evident in reduced catch rates of all population components. In addition, broad-scale reductions in prevalence of Bitter Crab Disease are consistent with declining productivity. The evidence suggests that a warming oceanographic regime underpins the decline in productivity and recruitment. However, other factors such as overfishing and increasing predation may be having localized impacts in some areas and have potential to exacerbate the rate of future decline.

5.6.2 Bottom-up versus Top-down Influences

Snow crab populations are undoubtedly susceptible to forces and interactions associated with many factors. Although this and a number of recent studies have shown bottom-up temperature influences to be the primary mechanism determining year-class strength, other processes certainly influence the subsequent biomass that becomes available to fisheries. This

study in no way intends to dismiss their relevance. Among a host of factors, mortality associated with over-exploitation does impact near-future fisheries (i.e. Mullowney et al., 2012), trawl fisheries do interact with snow crab on the seafloor (Dr. Paul Winger, unpublished data), disease does kill crabs (i.e. Shields et al., 2005, Mullowney et al., 2011), and large finfish consume snow crab in their diets. Furthermore, cannibalism has been shown to be an important regulator of snow crab populations in the northern Gulf of St. Lawrence, with early instars particularly susceptible to consumption by larger crabs (Lovrich and Sainte-Marie, 1997; Sainte-Marie and Labrance, 2002). Further, diet is a possible causative factor that we have not considered. The diet of NL snow crab has not been extensively studied, although Squires and Dawe (2003) highlighted the important contributions of polychaetes, pandalid shrimps, and capelin (*Mallotus villosus*) for individuals inhabiting waters off the northeast coast of Newfoundland. Although the abundance of shrimp has recently declined off the northeast coast (Orr and Sullivan, 2012), and capelin abundance has been perpetually low since the stock collapse in the early 1990s (DFO, 2011), there are no long-term diet data available from which to assess if these factors have influenced recent crab resource declines.

Despite these other influences on snow crab, the evidence suggesting temperature to be the primary driver of snow crab population dynamics is strong. It is the only factor that is consistent among regions having diverse levels of other factors. For example, in NL, the northernmost areas (i.e. Divisions 2HJ3K) have higher fishery exploitation rates, receive considerable levels of shrimp trawling, and have the highest rates of BCD. In contrast, the southern areas (i.e. Divisions 3LNOPs) have less trawling, low rates of disease, and cod stocks that did not decline to the same extent as the northern stock. Despite spatiotemporal variability

in all these factors, snow crab fishery catch rates have maintained oscillatory patterns linked to the climate signal (Figure 5.10) in all areas (Mullowney et al., 2013). Similar findings have been reported from other regions where large snow crab populations reside, with populations following climate signals despite spatiotemporal variability in other factors (Boudreau et al., 2011, Marcello et al., 2012).

The influences of bottom-up forcing are known to occur over large spatial scales in marine ecosystems (Shackell et al., 2009). In our case, the snow crab resource followed a similar trajectory of growth, and now decline, across all areas of the NL shelf. Declines in cold water coverage began several years earlier in northern Divisions (2J3K), thus it is consistent to expect a delay in fishery impacts in the southern Divisions (3LNOPs). The southern area fisheries have been able to extract greater amounts of crab yet consistently avoid soft-shell encounters (i.e. over-fishing) because of higher productivity in the southern areas resulting from the greater expanse of shallow, cold, bottom water. Nevertheless, a decline in recruitment into the exploitable biomass in the southern areas is anticipated as the effects of decadal-long warming begin to come to fruition. A recent recruitment pulse has now near-fully entered into exploitable size in these areas with no subsequent pulses evident (Mullowney et al., 2013).

Although cold water is evidently beneficial for early-life survival, it is debatable exactly what mechanisms govern this process and at exactly what stage the effect(s) occur. Szuwalski and Punt (2013) recently demonstrated a lagged effect of temperature on female snow crab recruitment in the Eastern Bering Sea, hypothesizing that temperature effects were exerted at larval stages, with survival influenced by food availability in the pelagic phase and during

subsequent advection to nursery grounds. In contrast, however, our data (based on best fit lags, see Mullowney et al., 2013) infer that the impact of temperature occurs following settlement, and we hypothesize temperature interacts with post-settlement metabolic demand to regulate early-life survival. Whatever the mechanism, it is clear that further research efforts should be directed at understanding this early-life bottleneck for snow crab.

Along with directly influencing year class strength, bottom-up forcing may also impact snow crab recruitment in other ways. For example, increasing temperatures might lead to increased abundance of finfish in cold-water ecosystems (Worm and Myers, 2003; Drinkwater, 2005; 2006; Wieland and Hovgard, 2009), and consequently predator regulation. However, the extent to which the abundance of predatory finfish increases is likely to be driven in indirect as well as direct fashions by temperature. Drinkwater (2005) found that population dynamics of northern cod were largely dependent on processes influencing primary and secondary production, and impacts on potential predator (i.e. deYoung and Rose, 1993) and prey (Frank et al., 1994; Rose and O'Driscoll, 2002) distributions are well known. Mullowney and Rose (2013) recently showed that a capelin deficiency in the diet has limited the growth of individuals in the northern cod stock, which has reduced growth in stock biomass and possibly recruitment. They posited that a positive response of the northern cod to warming temperatures has been mollified by poor feeding, especially on capelin, their former chief prey. Indeed, bottom-up influences of diet have been shown to be limiting capelin population growth (Obradovich et al., 2013), specifically due to a lack of euphausiids (Dalpadado and Mowbray, 2013).

Our overall goals are not only to better understand the dynamics of snow crab in NL waters, but to inform management on fishing and conservation strategies. Management cannot control the influences of bottom-up processes throughout the ecosystem, including the impacts on snow crab recruitment. However, under the scenario of an anticipated decline in snow crab biomass, and a fishing industry that remains largely dependent on crab, it is advisable to focus efforts on controlling potentially influential top-down interferences, even if they are not ascribed as the primary driver of snow crab population dynamics. Clearly, it is within the capability of management to control fishery exploitation rates as well as exert influence on factors such as interactions with trawling and seismic activities. In addition, the impacts of increasing groundfish, especially cod, on snow crab requires additional study. If there is a benefit from the extreme fishery, environmental, and community changes of the past decades, it is that it offers the range of contrasts needed to better understand the mechanisms that impact abundance and distribution of snow crab and other species in this northern shelf ecosystem. Ultimately, although we may understand the importance of bottom-up forcing on this species, we cannot control it. The only factors that can be controlled are fishing activities.

5.6.3 Outlook

The finding of climate as the primary driver of NL snow crab declines necessitates an exploration of events occurring in the environment. The recent broad-scale warming in the northwest Atlantic, coupled with events such as declines in cold water crustaceans like snow crab and northern shrimp (Orr and Sullivan, 2012) and increases in many finfish stocks, makes it seem highly plausible that we are on the cusp of or in the midst of a regime shift. Regime shifts

are rapid reorganizations of ecosystems from one relatively stable state to another. The ability to adapt to or manage regime shifts relies on fundamentally understanding their causes (deYoung et al., 2008). In the marine environment they are often associated with climate shifts (i.e. Biggs, 2009; Mueter et al., 2009), with impacts persisting for decades and changes in community productivity and structure occurring over large spatial scales. Fishing may also contribute to or even precipitate shifts, with interactions between climate, productivity, and hence sustainable fishing levels, a given (Rose, 2007). Regime shifts have been identified in many northern ecosystems from re-analysis of history (Anderson and Piatt, 1999; Hare and Mantua, 2000; Beaugrand, 2004; Tian et al., 2011) with the most pronounced one in the North Atlantic in the 1920s and 1930s (Drinkwater, 2006), whereby warm conditions persisted into the 1950s-1960s. This warming had profound impacts for fisheries throughout the North Atlantic, causing large poleward range extensions for many species (Edwards et al., 2013). It is plausible such a pattern could be repeated if recent warming persists. Trends in the broadest-based climatic indices of sea surface temperature incorporated in the Atlantic Multidecadal Oscillation (AMO) Index, a naturally occurring signal of low-frequency temperature variability incorporating latitudes north of the equator (Figure 5.12), generally reflect the historic patterns of regime shifts described in the literature, with multidecadal variability observed in the order of about 60 to 80 years (Drinkwater et al., 2013).

The AMO shows that broad-scale warming has recently occurred in the north Atlantic, but the future state of the ocean climate remains uncertain. Edwards et al. (2013) investigated the AMO drivers in a principal components analysis and found that the two warming phases of the 20th century have had similar hydro-biological impacts but there is a fundamental difference

with the current warming being driven more by the increasing monotonic temperature trend in the Northern Hemisphere. They concluded that the key question of when the current warm phase of the AMO will begin to decline remained elusive, as does a clear understanding of the relative future influence of the natural low frequency signal versus the anthropogenic-induced warming phenomenon. Cannaby and Husrevoglu (2009) estimated the peak in the AMO may occur around 2025, roughly based on a 60 year cycle, while Holliday et al. (2011) predicted the AMO has peaked and that coming decades will bring cooling temperatures. If both the natural low-frequency and anthropogenic-forced monotonic warming signals persist, a scenario of possible cooling during the next negative phase could be followed by rapid warming during the next positive phase. Future improvements in capacities to predict ocean climate would greatly help improve expectations and management of the snow crab resource beyond the 8-10 year predictive capacity afforded by current knowledge. Drinkwater et al. (2013) found that many species which have only been researched in recent decades suggest a multi-decadal effect linked to climate, but short time series makes the connections impossible to confirm. Nevertheless, initial indications from all studied ecosystems are that snow crab responds strongly to bottom-up processes with relatively long lead-time to the fished stock. This feature is fundamental to management of the species and has potential importance to studies of climate and shifts in community regimes in northern ecosystems.

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5.8 Figures

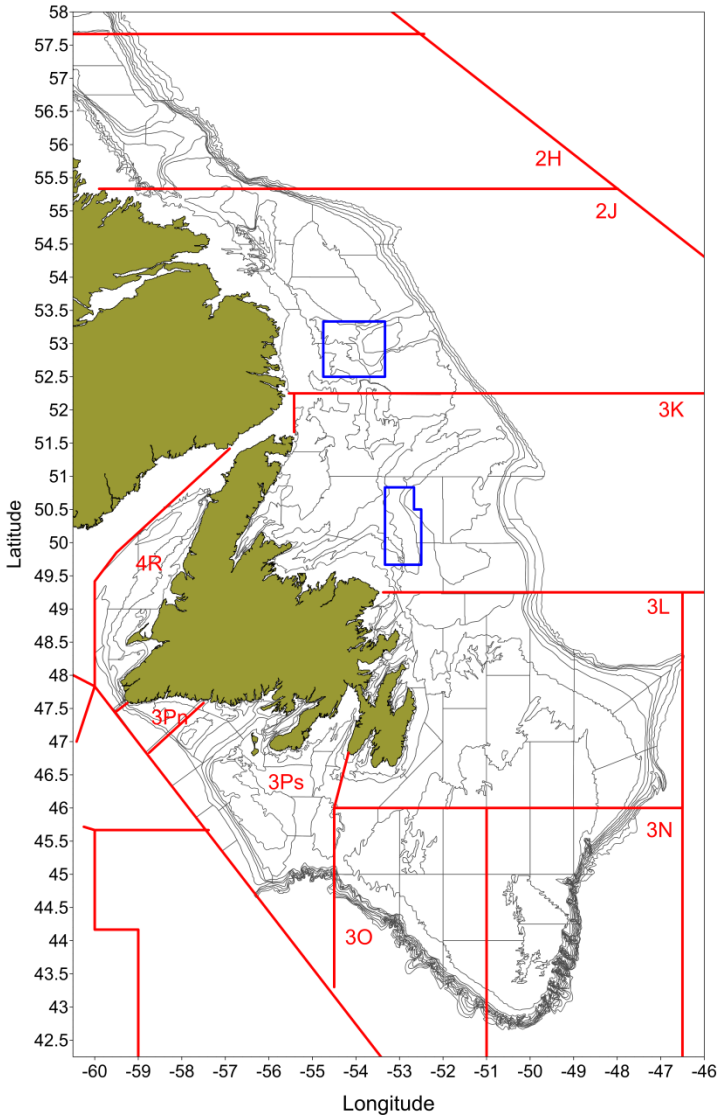

Figure 5.1. Map of the Newfoundland shelf showing Northwest Atlantic Fisheries Organization Divisions (NAFO- red), trawl closures (blue), and depth strata of the multi-species trawl surveys (grey).

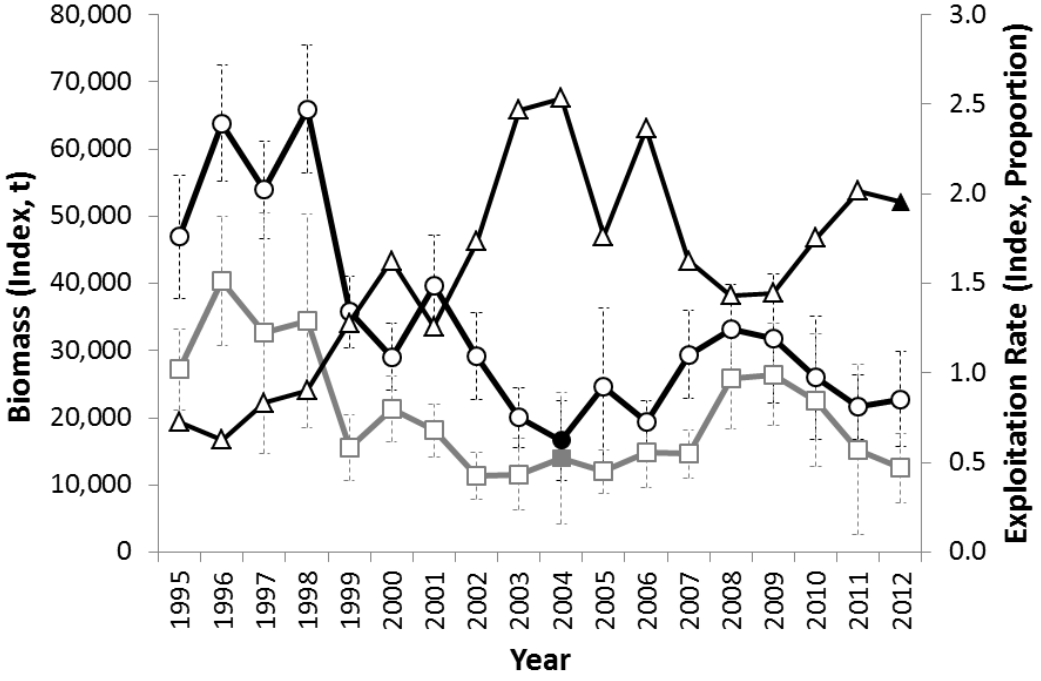

Figure 5.2. Exploitable Biomass (black circles), Pre-recruit Biomass (gray squares), and Exploitation Rate (black trianges) Indices for Divisions 2HJ3KLNO. Error bars are 95% confidence intervals. The 2012 exploitation rate point estimate assumes the entire 2013 quota will be taken. The solid symbols in 2004 indicate incomplete surveys.

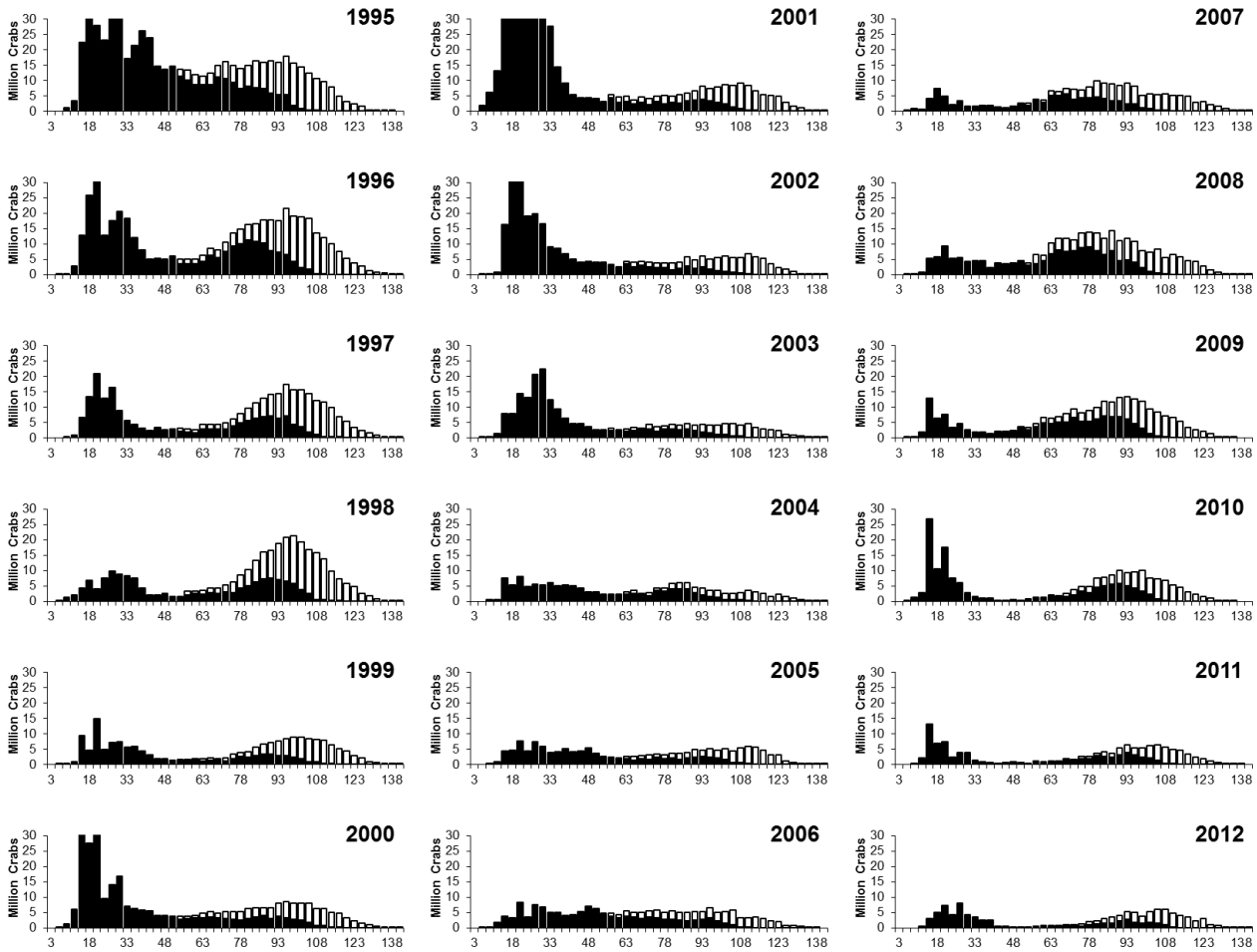

Figure 5.3. Annual Divisions 2HJ3KLNO fall trawl survey abundance indices of male snow crab by size. Adolescents in black and adults in white. X-axis units are carapace width (CW).

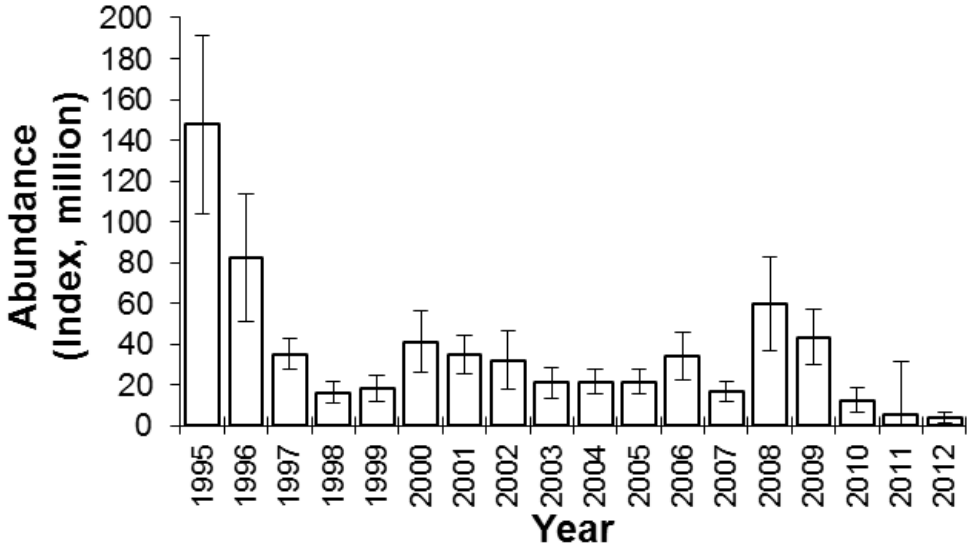

Figure 5.4. Annual Divisions 2HJ3KLNO abundance index of mature female snow crab. Error bars are 95% confidence intervals.

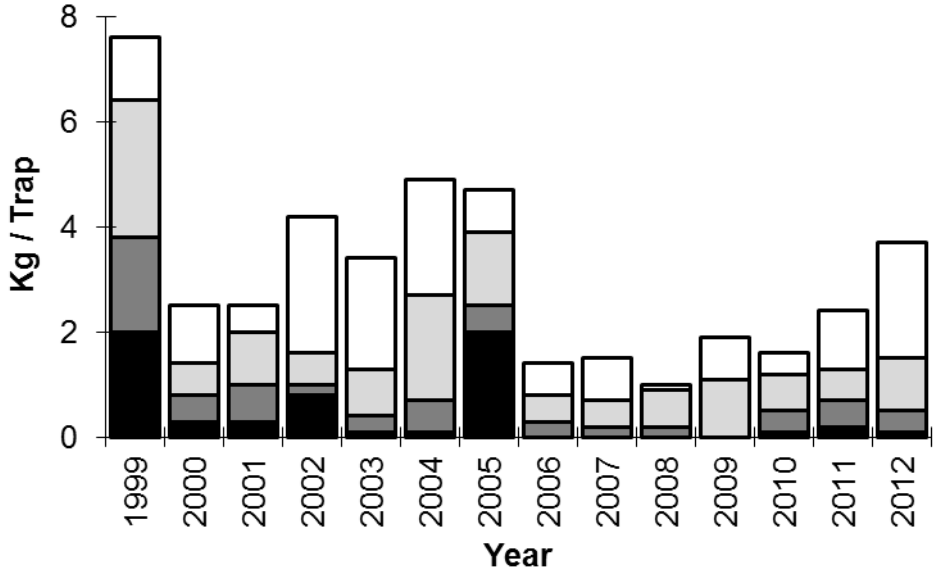

Figure 5.5. Annual observed catch rates of soft-shell crab in the fishery by NAFO Division (2J-white, 3K-light gray, 3LNO-dark gray, 3Ps-black).

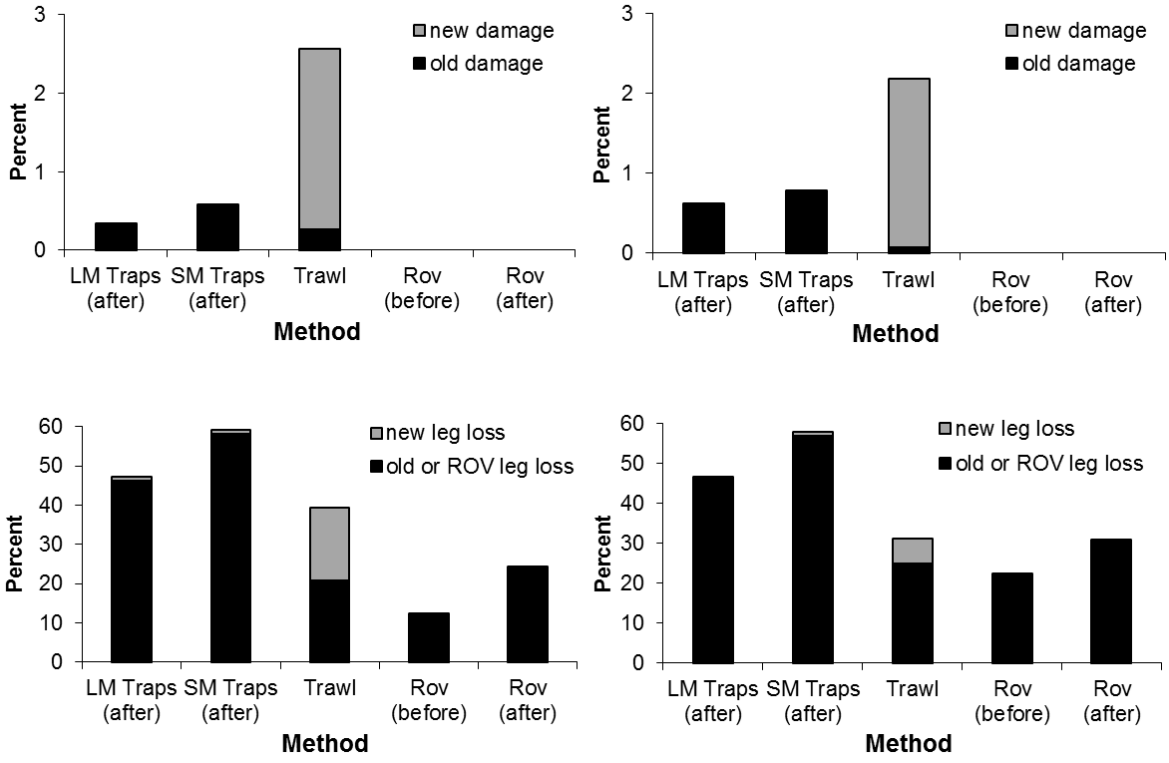

Figure 5.6. Crab damage caused by trawling from 2007 St. Mary's Bay experiments. Top panels show Carapace damage (left=outer corridor, right-mid corridor) and bottom panels show leg loss (left=outer corridor, right=mid corridor). LM traps indicates large-mesh traps, SM indicates small-mesh traps.

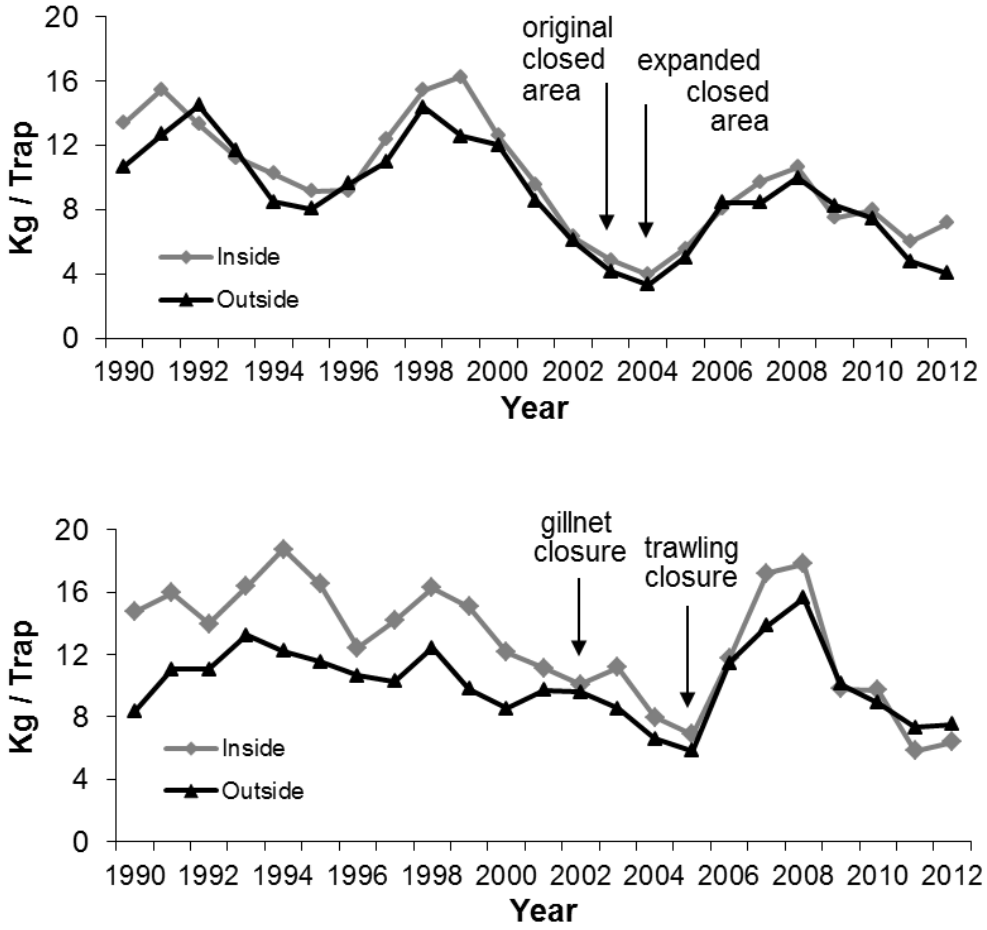

Figure 5.7. Annual logbook-based catch rates of snow crab inside versus outside trawling closure areas. Hawke Box (Division 2J – above) and Funk Island Deep Box (Division 3K – below).

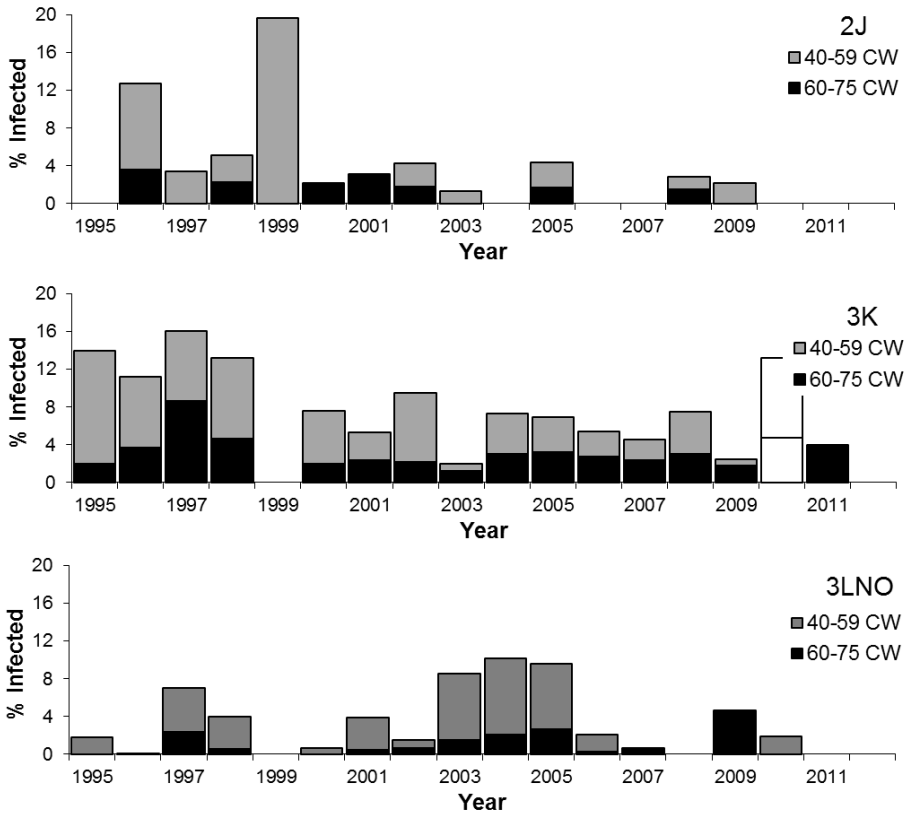

Figure 5.8. Annual trends in Prevalence of Bitter Crab Disease from fall multi-species trawl surveys. 2010 value in Division 3K deemed anomalous (see Analysis – Disease section of text).

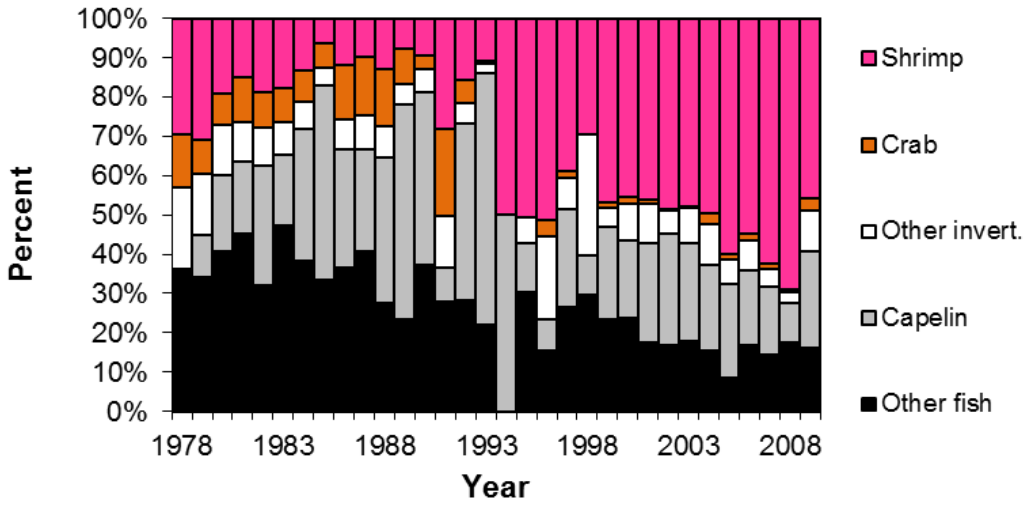

Figure 5.9. Annual composition of northern cod diet from fall multi-species trawl surveys in Divisions 2J3KL. Data taken from Dawe et al. 2012a. The y-axis is the percentage contribution by weight. Sampling of stomachs was length-stratified for all sizes of cod. Further details available in Dawe et al., 2012a.

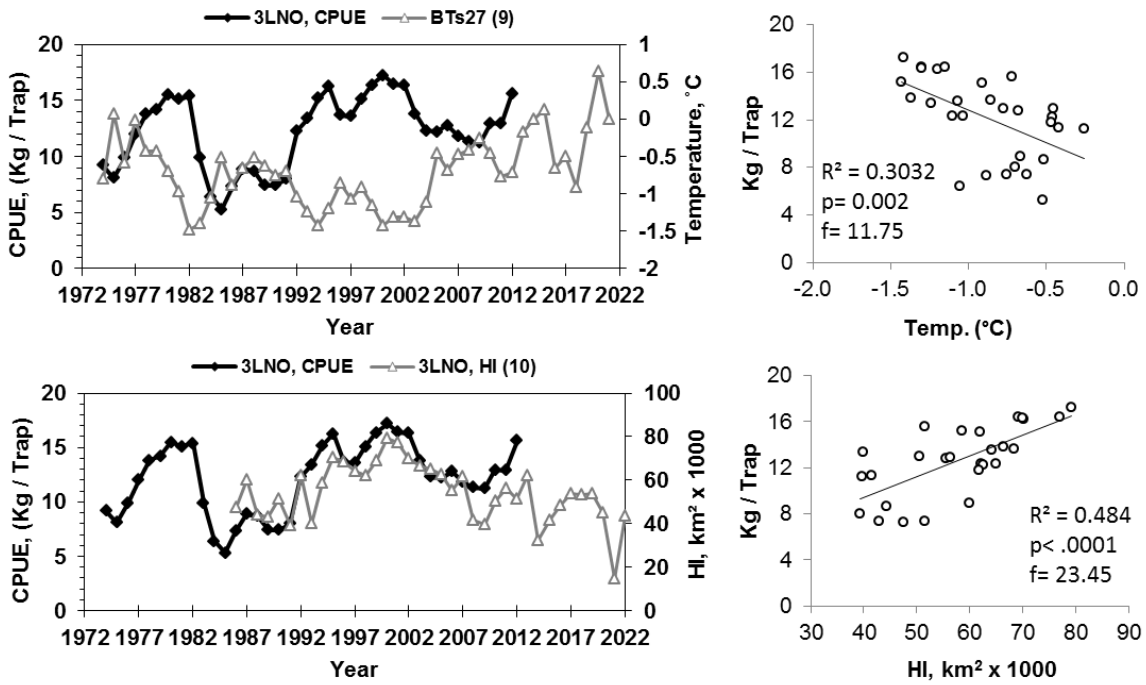

Figure 5.10. Lagged relationships of Station 27 fall bottom temperature vs. Division 3LNO snow crab CPUE. Top panels show relationship of fishery CPUE versus raw bottom temperature and bottom panel shows relationship of fishery CPUE versus areal extent of <1°C water (HI=habitat index). Right panels show linear relationships and significance.

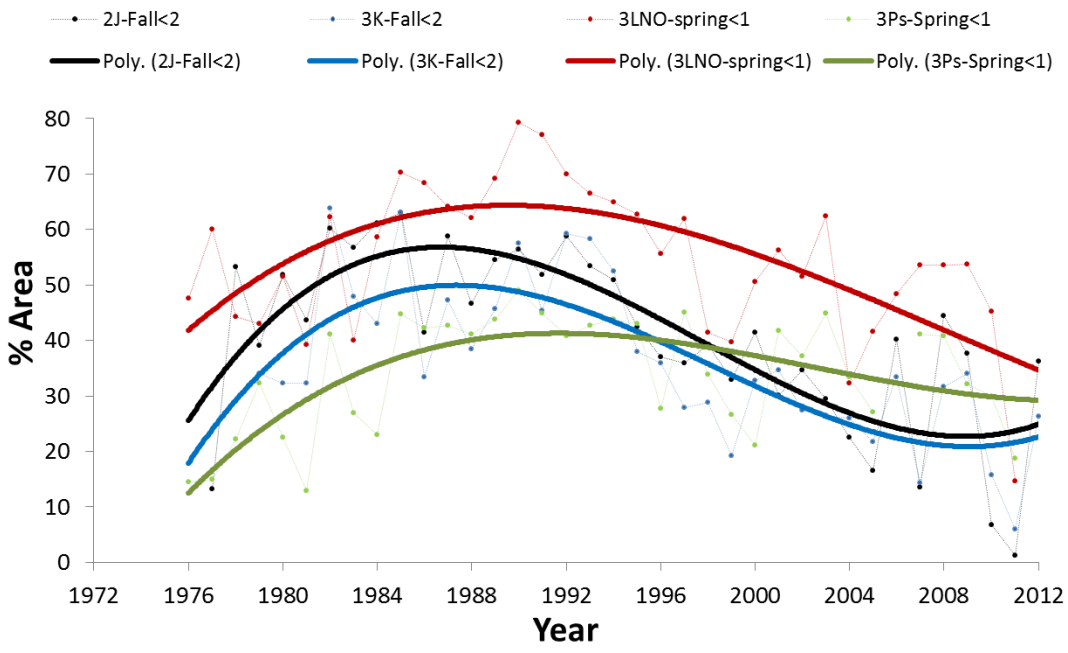

Figure 5.11. 3rd Order Polynomial Regression Models of Snow Crab Thermal Habitat Indices. Data acquired from multi-species trawl surveys.

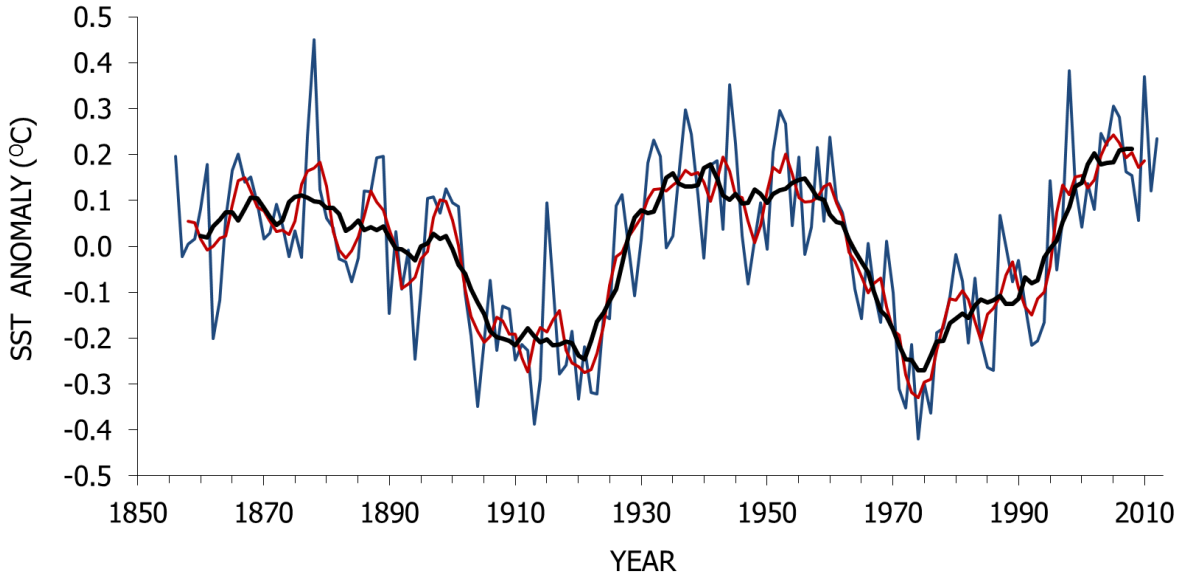

Figure 5.12. The annual Atlantic Multi Decadal Oscillation Index (blue line). The red and black lines are the 5 and 9 year running averages.

Chapter 6

Synthesis and context of findings

6.1 A Transitioning Ecosystem

6.1.1 Current Status

The research presented in this thesis has addressed key events occurring along the NL shelf in recent decades and provides a basis for inferences on the forthcoming direction of the ecosystem and fisheries. Simply put, the NL shelf is in a period of change. Collectively the research results indicate that the direction of dominant control is shifting from a bottom-up regulated ecosystem toward one with additional top-down influences. Change is a constant and fundamental feature of all ecosystems, but the level of change potentially forthcoming along the NL shelf is larger than experienced in recent decades and appears to be the most pronounced shift in trophic control since the early 1990s.

As hypothesized, the results of the research chapters of this thesis support earlier contentions that the NL shelf ecosystem has been strongly regulated by bottom-up processes over the past two decades (DFO, 2014; Buren et al., 2014a;b). Moreover, my research advances these notions by identifying specific bottom-up links between dominant apex and pelagic finfish populations that were subject to food-limitation (cod and capelin) and adds snow crab regulation, primarily

by temperature. Although the research suggests the NL shelf is in a period of transition, it cannot explicitly quantify the extent to which a trophic control shift will occur.

My supposition of a current shift in trophic control is consistent with other emerging research showing recovery in the biomass of northern cod (Rose and Rowe, 2015) and northern shrimp having recently come under increased predation control (DFO, 2016a) as some have described as occurring historically in the presence of large finfish abundances (Worm and Myers, 2003; Parsons, 2005; Savenkoff et al., 2006; Greene et al., 2009).

More generally, the coupling of a trophic control shift with warming suggests that the NL shelf may be entering or is in the early stages of a regime shift, one favouring temperate finfish over cold-water crustaceans. However, identifying regime shifts in real time is subjective. For now, it can be concluded that climate warming is having a profound impact on the NL shelf ecosystem and fisheries. My research suggests that above all else the response of capelin to the warming will determine the forthcoming state of this ecosystem, but impacts on many species are to be expected.

Regarding the fisheries, the industry should expect to diversify beyond cold-water shellfish and toward temperate finfish over the next decade. However, the extent of re-alignment and diversification necessary will depend on how the ecosystem and its components respond over the next decade.

6.1.2 Processes Affecting Transition

After the declines in capelin and cod in the early 1990s, and the dominance of shrimp and snow crab in the fisheries since then, the ecosystem and fisheries now appear to be transitioning to a state more closely resembling historical norms (see Rose 2004; 2007). As evident in much of my research, this transition appears to be a consequence of ocean warming. My research shows that warming has contributed to the recovering state of the focal apex species, northern cod (Rose and Rowe, 2015; Cadigan, 2016a;b). The study on juvenile northern cod in Chapter 2 revealed that growth at young ages is strongly related to temperature, while the studies on adult cod in Chapter 3, and important drivers affecting capelin in Chapter 4, demonstrate that temperature acts indirectly to influence cod through impacts on phenomena such as sea ice and spring bloom dynamics and low trophic level productivity. With warm conditions generally beneficial for enhanced productivity at low trophic levels as well as capelin success, warming is likely to be overall advantageous for productivity of most finfish stocks along the NL shelf. These results are consistent with earlier predictions for cod and other species based on ocean climate change (Drinkwater, 2005; Rose, 2005).

The underlying rationale on why the ecosystem is transitioning toward temperate finfish is that food-limitation is easing and overall trophic throughput in the ecosystem is increasing. In Chapter 4, it was demonstrated that the key energy conduit, capelin, appears to have been food-limited for most of the past two decades due to a prolonged mismatch with the spring bloom and a relatively low probability of access to critical zooplankton species such as early-stage *Calanus finmarchicus* for first feeding. The match-mismatch of capelin with the spring

bloom is arguably the most important phenological relationship in this ecosystem. I showed that not only are early blooms under warm conditions associated with overall higher production of zooplankton, they are also associated with a more preferential zooplankton community composition for first feeding capelin than delayed blooms.

Throughout the analyses the research suggested that the success of cod in the northern stock is highly dependent on the success of capelin. Consistent with this, recent evidence from DFO fall multi-species trawl surveys shows a large increase in the contribution of capelin to the diet of northern cod >35 cm total length in the past three years in Divisions 2J and 3K (Figure. 6.1), where stock recovery has been greatest and condition levels most improved (Rose and Rowe, 2015). A key aspect of this dependence in northern cod is that no readily available substitute for capelin exists as it does in other stocks, where lipid-rich herring or sand lance (*Ammodytes dubius, A. americanus*) are more numerous. In any event, the dependence on capelin suggests that the rebuilding in northern cod will only be sustained if capelin recovery is also sustained. Further research is recommended to determine how much capelin is required to feed a rebuilt population of northern cod and other predators.

Converse to positive impacts of warming on primary and secondary production and pelagic and apex finfish, snow crab productivity has been drastically reduced with warming over the past decade. The conclusion in Chapter 5 of temperature regulation of snow crab can be seen in all major assessment divisions incorporated in the snow NL snow crab assessment (Figure. 6.2). A thermal habitat index, defined as a three-period moving average of the areal extent of cold bottom water (<2°C in Divs. 2HJ, 3K, and <1°C in Divs. 3LNO, 3Ps [derived from annual multi-

species trawl surveys]) lags against future fishery catch rates with strong correlations in all areas. My research indicates that snow crab have been largely under bottom-up thermal regulation in the absence of high predatory finfish abundances for the past two decades. This conclusion is consistent with the most recent assessments of this stock (DFO, 2016b). The overall abundance of snow crab along the NL shelf was at its lowest level in two decades in 2015 (unpublished data).

6.1.3 Future Ecosystem State

If capelin abundance is not limiting and the fishery does not prematurely interfere, the ecosystem is headed toward a finfish dominated community. My research suggests the prolonged poor state of cod was indicative of a lipid deficiency, as advanced by Rose and O'Driscoll (2002). In Chapter 3, I showed that northern shrimp lack lipids relative to other prey species. On a diet dominated by shrimp for most of the past two decades (Dawe et al., 2012a), stock productivity has been very poor. However, the results from experimental feedings in Chapter 3 showed that northern cod are capable of regaining growth rates and condition levels similar to historic norms if the forage base is sufficient.

Although the northern cod stock trajectory is likely to reflect that of capelin, the composition of the future trophic community remains somewhat uncertain. Other temperate finfishes could become more prominent, but few species do well in the generally colder waters of 2J3KL. This contrasts with other ecosystems, such as southern Newfoundland in NAFO Subdivision 3Ps, where the prey species complex is more diversified, and Silver Hake (*Merluccius bilinearis*) has recently emerged as the most abundant apex predator (DFO, 2015).

Increasing temperature and predation potential do not bode well for snow crab. Although predation control has not been the primary driver of stock abundance to date, a recent analysis showed consumption by predatory finfish has increased markedly in the past three years (DFO, 2016b). Such a change is likely to have been reinforced by the increase in large cod (Rose and Rowe, 2015). It is expected that along with a direct negative effect on snow crab productivity, warming temperatures will exert an indirect effect in the form of increased top-down predation control.

The overall rate and magnitude of the current and forthcoming trophic control shift is unknown. Perhaps the best inference to be drawn is from temperature indices. With the present rate of change being more gradual than occurred during the late 1980s / early 1990s regime shift, forthcoming changes would not be expected to be as rapid or substantial.

Regarding the fishery, although prospects for fishing cod are rising, they should be tempered until the stock becomes more firmly established over its former range, and although prospects for the snow crab fishery are diminishing, they are not fully lost. Successful fisheries for temperate finfishes such as Pacific Cod (*Gadus microcephalus*) and Walleye Pollock (*Theragra chalcogramma*) have co-existed with fisheries for cold-water snow and tanner (*Chionoecetes bairdi*) crabs in the Eastern Bering Sea of Alaska for decades, even through regime shifts (Benson and Trites, 2002). However, the industry must be adaptable to changing environmental conditions and harvest levels.

6.1.4 Bottom-up Regulation For Decades

Many of the initial papers explaining the collapse of northern cod demonstrated the direct and resonating impacts of overfishing (Hutchings and Myers, 1994; Myers et al., 1996; 1997; Hutchings, 1996), although deYoung and Rose (1993) were quick to implicate environmental factors. More recently, several authors questioned if the role of synergistic environmental factors had been thoroughly considered. For example, Rothschild (2007) found the broad-scale decline in productivity of Atlantic Cod stocks reflected a major perturbation in the forage base, while Hilborn and Litzinger (2009) modelled surplus production rates to arrive at a conclusion that fishing alone could not possibly account for the sudden productivity loss. One striking observation was that virtually the entire finfish community collapsed and not just those stocks subjected to directed fishing or by-catch (Atkinson, 1994;, Gomes et al., 1995). Recent reviews have concluded that multiple factors, including both fishery and environmental impacts, caused the decline (Rice, 2006; Rose, 2007; Lilly, 2008).

The Northern Cod Assessment Model (NCAM – Cadigan, 2016a;b) is the currently accepted model for assessment of northern cod. It incorporates a myriad of datasets including fishery landings, surveys from trawls, gillnets, long-lines, and acoustics, as well as broad-scale tagging information. The tagging data allow it to partition total mortality (*Z*) into natural (*M*) and fisheries-induced (*F*) sources. The NCAM outputs reveal three periods with differing levels of mortality and causes (Figure 6.3). Prior to about 1990, *F* equalled or exceeded *M* for fish above age 4. During and following collapse, from about 1990 to 1994, both *F* and *M* increased sharply in most ages of fish. However, the increase in *M* was much greater. Since stock collapse, with

little exception, *M* has exceeded *F* for virtually all fish in the stock. Although the NCAM indicates that natural causes have been a major driver of cod survival since about 1990, some caution is warranted in interpreting the relative magnitude of *M* and *F* as tags not returned from fish captured in the fishery are partitioned as natural mortality, thus creating an upward bias on *M* and downward bias on *F* (personal communication, Dr. Noel Cadigan). As the level of unreported tags is not certain, the extent of this bias is not known. Nonetheless, the NCAM model verifies earlier reports that high natural mortality along with excessive fishing caused the collapse of the northern cod.

My research is consistent with high natural mortality having contributed to the collapse and belaboured recovery of the northern cod stock, and provides evidence for plausible mechanistic avenues through temperature-induced food limitation. Indeed, such bottom-up processes are almost certain to have affected northern cod populations for centuries. For example, Rose (2004) examined a 500 year time series of documented history for Newfoundland cod and found declines in the mid-to-late 19th and 20th centuries were best explained by a model incorporating both fishery and climate variables, with neither realm of factors alone producing tight fits to survey data or historical knowledge about the fishery. Interestingly, like the NCAM outputs, he described temporal differentiation between fishing and climate effects, with declines during 1800-1880 caused by low productivity, a collapse in the 1960s caused by overfishing, and the late 1980s – early 1990s collapse caused by both. Most recently, in a bioenergetics model, Buren et al., (2014) found that a lack of capelin along with continued fishing on northern cod explained poor post-collapse performance, with other factors such as predation by harp seals being marginal.

Beyond cod, a litany of recent works have established the linkage between cold water conditions and high snow crab productivity for the largest populations throughout Atlantic Canada and the Eastern Bering Sea (Boudreau et al., 2011; Marcello et al., 2012; Windle et al., 2012; Szuwalski and Punt, 2013; Émond et al., 2015). Similarly, for NL capelin, bottom-up regulation by various climatic phenomena have long been viewed as the most important regulators of population dynamics (Frank and Leggett, 1981; Leggett et al., 1984; Carscadden et al., 2001; 2013; Rose, 2005). The importance of bottom-up regulation of snow crab and capelin may be more apparent than for northern cod as neither stock has been knowingly decimated by fisheries.

6.2 Management Considerations

6.2.1 Control the Controllable

Although bottom-up processes have profound impacts on the NL shelf ecosystem, particularly in recent decades, they do not operate in isolation. At times, bottom-up processes are not even the dominant factors affecting the fish community (Rose, 2004). Regardless of the state of the ecosystem or direction of trophic control, there is little that fisheries management can do to control bottom-up processes. The fishery is the only variable directly controllable through management.

Northern marine ecosystems such as the NL shelf generally feature a low diversity of prey fishes and slow growth and maturation of apex predators, compromising their resiliency to fishing (Frank et al., 2006; 2007). Relative to more temperate ecosystems, the impacts of overfishing

may be more severe and last longer. Ramifications of overfishing concomitant with stock collapse long-resonated in northern cod. Intrinsic population responses consistent with depensation occurred (Shelton and Healy, 1999; Frank and Brickman, 2000; Rowe and Hutchings, 2003; Rose, 2004; Buren et al., 2014). Even with the removal of most fishing and the onset of warming in the years following collapse, productivity continued to decline. Some authors have suggested that early maturation indicative of rapid genetic evolution may have occurred in the stock (Olsen et al., 2004; Hutchings, 2004). Finally, even small-scale fisheries on the stock since collapse have been shown to have contributed to delayed recovery (Shelton et al., 2006; Buren et al., 2014).

Although the environment has strong control over commercial fish stocks and community composition, the exploitation of these stocks can interfere with natural processes and stock fluctuations. Inevitably, socio-economic circumstances and risk tolerance are key factors for management to consider in determining fishing quotas. Moving forward, in addition to recent direct study of the northern cod stock (i.e. Rose and Rowe, 2015), there is precedent from the Barents Sea to suggest that northern cod removals should remain low in the short-term while stock rebuilding is still in the initial stages.

6.2.2 Barents Sea – Similar Collapse, Different Outcome

The Northeast Arctic (NEA) cod stock in the Barents Sea occupies a similar ecosystem as the NL shelf, with many species of prey and predators in common with northern cod (Lilly et al., 2008). Historically, these two stocks have been among the largest. The NEA stock underwent an initial large decline from about 2 million t in the early 1970s to its lowest observed level of less than 1

million t in 1980. The stock biomass briefly recovered to about 2 million t in 1992 but subsequently declined throughout the 1990s back to about 1 million t in 2000. In stark contrast to the northern cod, over the past decade, the NEA cod stock has undergone a large recovery, with stock biomass achieving over 3.5 million t by 2010 (Kjesbu et al., 2014). The NEA stock is presently the largest Atlantic cod stock and supported a fishery of about 1 million t in 2010 (Kjesbu et al., 2014).

Both the northern and NEA cod stocks were subjected to intensive fisheries, extreme environmental changes, and capelin perturbations concomitant with collapses (Lilly et al., 2008). Differences in recovery outcomes between the two stocks have been attributable to both management actions and environmental factors. Lilly et al. (2008) described how initial indications of decline in the two stocks were met with minimal reductions of fishing on the northern cod stock and considerable reductions in fishing on the NEA stock. These actions were followed by the North Atlantic Oscillation entering into a strong positive phase which created unfavourably cool conditions in NL and favourably warm conditions in the Barents Sea. This confluence of events did not allow the northern cod to recover while the NEA stock began to increase. Kjesbu et al. (2014) described how in the Barents Sea, a harvest control rule established in 2004 that set a minimum threshold biomass limit (B_{lim}) of 460 thousand t and maintained the exploitation rate at F=0.3-0.4 allowed fishing mortality to remain low and promote recovery. However, they also found that the Barents Sea benefitted from favourable environmental conditions.

During the past decade, the Barents Sea has warmed to record high temperatures and the habitual range of cod has expanded considerably (Kjesbu et al., 2014). Coincidentally, there was a substantial increase in capelin biomass in 2008 that still persists (Figure 6.4a). NEA cod have exploited prey species over a very broad geographic range (Johannesen et al., 2012; Kjesbu et al., 2014). The complex of abundant prey species available to NEA cod is more diverse than for northern cod. In particular, in years when capelin abundance is low, herring (*Clupea harengus*) abundance tends to be high (Figure 6.4a). Nonetheless, despite a higher buffering capacity created by additional prey fishes in the ecosystem, with its recent range expansion the NEA cod stock appears to have primarily benefitted from consistent access to capelin. The NEA cod diet has become unusually and favourably dominated by capelin in recent years (Figure 6.4b).

Despite the fortunate environmental factors benefitting NEA cod, Kjesbu et al. (2014) showed that prudent management was the main criterion of success with simulations suggesting that the NEA cod stock would have not recovered to its current high level had harvest rates been more aggressive during initial stages of stock rebuilding. The logic of cautious exploitation to promote recovery extends beyond apex predators into their forage domain. For example, no fishing on capelin was permitted from 2003-2008 during the recovery period of NEA cod (Gjøsæter et al., 2015).

The recovery of the NEA cod stock demonstrates how effective management can mitigate negative impacts under unfavourable environmental circumstances or amplify positive impacts under favourable environmental conditions. It also re-iterates why DFO management is advised to keep removals on the northern cod stock low during this initial recovery phase.

6.2.3 Caution Despite Science

6.2.3.1 Capelin

The practice of 'fishing down the food web' has been argued to promote ecosystem instability and be unsustainable (Pauly et al., 1998). Given the vital role of capelin in the NL shelf ecosystem it is reasonable to question if a fishery should be prosecuted on this species, particularly as historical fisheries often selected for gravid females (DFO, 2010).

There has been a commercial capelin fishery along the NL shelf since the early 1970s (DFO, 2010), but an estimated 20,000-25000 t were taken annually for bait, fertilizer, and other uses for decades prior (Templeman, 1968). Throughout the 1980s, the catch of capelin averaged 4.3 % of the estimated mature biomass in Division 3L (Shelton et al., 1992), with peak landings of about 80,000 t in 1988-1990 (DFO, 2010). It is difficult to accurately quantify exploitation rates on the capelin stock due to uncertainties in biomass estimation and fishery practices, but recorded landings have remained low, at about 10,000–30,000 t annually since the early 1990s, while operating under a management approach of exploiting <10 % of the estimated spawning stock biomass (DFO, 2010).

Carscadden et al. (2001) suggest that fishing has never been a significant factor influencing the population biology of capelin along the NL shelf as the magnitude of removals by the fishery pales in comparison to consumption by predators in the ecosystem, which is orders of magnitude higher (Winters and Carscadden, 1978; Turuk, 1978; Carscaden et al., 2001). This aligns with a scientific view that capelin abundance and distribution are predominately

environmentally-driven (see references in section 6.1.4). Accordingly, the scientific literature from NL does not serve as a strong basis to completely prohibit a fishery on capelin.

In the Barents Sea, major fisheries for capelin have occurred for decades, and in relative terms fishery exploitation has been more aggressive than in NL. Annual landings in the order of 1.5-3.0 million t in the 1970s to mid-1980s represented a significant portion of the estimated standing stock biomass, which was about 3-6 million t annually during that period (Gjøsaeter, 1998). Since the 1990s, the Barents Sea capelin has been managed by a harvest control rule that aims to keep the probability of the spawning stock biomass falling below a limit (B_{lim}) of 200,000 t at $p<0.05$ (Gjøsaeter et al., 2015). Interestingly, estimates of consumption by cod are factored into the probability of the biomass following below B_{lim}. Landings in the range of 0-900 thousand t since the 1990s have represented about 0-40% of the mature stock size. There has been no fishing in years following stock collapses (Gjøsaeter et al., 2015).

There have been three collapses of the Barents Sea capelin since the early 1970s; one during the early 1980s, one during the early 1990s, and one during the mid-2000s (Hjermann et al., 2004; Gjøsaeter et al., 2016). In a review of competing hypotheses, predation on larvae, particularly by herring, was ascribed as the main cause of collapses (Gjøsaeter et al., 2016). However, predation alone does not fully explain the stock collapses and some have suggested overfishing could have contributed (Gjøsaeter, 1994; Hjermann et al., 2004). However, Gjøsaeter et al. (2016) largely dismissed fishing as highly influential because of high larval production at the onset of each collapse. Like NL, the prevailing scientific view is that the

Barents Sea capelin stock is predominately regulated by environmental factors (Gjøsaeter, 1994; Gjøsaeter et al., 2002a; Carscadden et al., 2013; Gjøsaeter et al., 2016).

The scenario poses a challenge to management. Capelin is the most critical conduit in the NL shelf ecosystem and the stability of upper trophic levels is heavily reliant on it, yet there is little scientific basis in the literature for prohibiting a fishery. Considering the other scenario being presented, whereby the NL shelf ecosystem is transitioning toward top-down control and there are likely to be increased demands on capelin from predatory finfish, my advice is to keep removals low. The fishery is all that can be controlled, even if it is not the most important factor affecting capelin productivity. There remain uncertainties surrounding the impacts of fishing on this resource, and indeed precedent from the Barents Sea whereby a fishing moratorium on capelin during 2003-2008 (Gjøsæter et al., 2015) was coincidentally timed with NEA cod recovery, to suggest that in the spirit of the Precautionary Approach uncertainties on the outcomes of prosecuting fisheries warrant caution in management.

6.2.3.2 Snow Crab

Like capelin, most literature from NL suggests population dynamics of snow crab are not primarily regulated by fishing and a strong case can be made that the management regime is sufficiently cautious. Further, unlike capelin, this species contains many biological attributes that appear to create a relatively high level of resilience to fishing.

Two key components of the snow crab management system geared toward protecting stock reproductive potential are requirements for large mesh (5.25” [133 mm]) pots in the fishery and the restriction of exploitable crabs to males ≥95 mm carapace width. The 133 – 140 mm

mesh size used in pots in the fishery (most harvesters use larger than minimum required size) avoids capture of most sub-legal-sized crabs (Mullowney et al., 2015).

Using the 1995 Divisions 2HJ3KL population distribution from the fall multi-species trawl survey in Figure 6.5 as an example (because it contained the overall highest abundance of crabs for any survey year), cautious management is evident. A key factor in management is the sexual dimorphism in this species, with females terminally molting at smaller sizes than males. All females are below legal-size and virtually immune from capture in the fishery (Mullowney et al., 2015). Coincidentally, males terminally molt into adulthood over a broad size range (Dawe et al., 2012b) and a large portion of adult males is also immune from capture by fishing. Further, adolescent males are capable of successfully mating females, and finally, females store sperm and can produce multiple clutches of viable eggs from a single mating event (Sainte-Marie, 1993). In the 1995 example, 9.5% of the total survey catch of snow crab constituted exploitable males. However, that is a gross overestimate as the distribution has not been corrected for size-selective catchability by the survey trawl ('*q*'), for which exact specifics are unknown but is highest on largest crabs (Dawe et al., 2010).

Evidence for the suitability of management measures in protecting reproductive potential may best be judged by an examination of female egg clutches (Mullowney et al., 2015). With over 80 % of mature females carrying full clutches of viable eggs in all areas and years over the past two decades, no matter the state of the exploitable biomass (Mullowney et al., 2015), the current prevailing scientific view is that management measures sufficiently protect stock reproductive potential in the presence of large-scale fisheries.

Recent evidence from the Eastern Bering Sea is suggesting that large old-shelled adult males (i.e. 'old' crabs) targeted by the fishery are spatially segregated from most breeding females and may not constitute prime breeders. Rather, they appear to emigrate away from females (Kolts et al., 2015). A similar phenomenon is seen along the NL shelf, in particular the Grand Bank (Divisions 3LNO), where the largest portion of the NL snow crab resource resides. There, since 1995, an analysis of depth distribution of large adult males during spring when mating occurs suggests a high degree of spatial separation from large mature females (Figure 6.6). Not only does the snow crab fishery target a very small portion of the population, it is not certain that the component targeted is of critical importance to reproduction.

Despite the prevailing scientific view that the fishery is not the dominant driver of population dynamics of snow crab, there is risk for fisheries to induce serious harm to the resource. Specifically, it is possible that excessive size-selective fishing could reduce genetic mixing in the stock, as has been known or suspected to occur in some heavily exploited marine species (Smith et al., 1991; Stephenson and Kenchington, 2000; Hutchings, 2004). This possibility may be particularly high in snow crab, which features limited diversity in its genetic portfolio (Merkouris et al., 1998). Intuitively, genetic forcing by fishing would most likely be toward smaller crabs. However, this possibility remains theoretical and current evidence in the literature shows that size is a plastic phenotypic trait regulated by temperature (Orensanz et al., 2007; Burmeister et al. 2010; Dawe et al., 2012b).

Like capelin, one could argue based on scientific evidence that fisheries for snow crab have little impact on population dynamics or overall ecosystem function and that sufficient restraint is

already being practiced. However, like capelin, the management advice I offer is to be cautious. Again, there remain uncertainties and unknowns surrounding the impacts of fishing on this resource, which warrants being cautious in management. The stock is clearly in decline (Mullowney et al., 2015; DFO, 2016b) and despite the fishery not being ascribed as the dominant driver of the decline, as productivity has diminished and recruitment of snow crab into the fishery been reduced in recent years , quotas have been reduced (DFO, 2016b).

6.3 Climate Considerations

6.3.1 Short-Term and Small-Scale Variability

How can the ecosystem be transitioning toward temperate finfish species when recent winters have been so harsh? How can snow crab catch rates in the biggest and most important area along the northern Grand Bank be near all-time highs if the resource is in decline (Mullowney et al., 2015; DFO, 2016b)? These events reflect short-term and small-spatial scale environmental processes.

Patterns of change in important ecosystem drivers are not normally linear or unidirectional. Virtually every index of environmental forcing factors examined in this thesis was characterized by either a high degree of short-term variability or an oscillating pattern. Paradoxically, it can be cold during warm periods and localized populations can thrive while stocks are in decline. In fact, the northern cod fishery constitutes a classic example of how fishery catch rates can increase on aggregated populations while stocks are in decline (Walters and Maguire, 1996; Rose and Kulka, 1999; Rice, 2006). This appears to be the case with the snow crab, which has

become highly localized into areas where the fishery is performing well (Mullowney et al., 2015; DFO, 2016b).

Converse to dangers associated with allowing short-term or small spatial scale variability to mask broad-scale signals, there is also danger in dismissing their influence, as they serve to add uncertainties and compromise predictive capacities. In this regard, climatic events occurring in NL in recent years must be mentioned, as they have the potential to affect the degree and pace over which an ecosystem transition can or will occur.

The last two years (2014-2015) have been cold and initial analysis of their impacts appear fully consistent with the resonating directional effects of important ecosystem processes detailed in the research chapters of this thesis. In short, the NAO index has been strongly positive in most months since the winter of 2013 (Figure 1.4), sea ice coverage during 2013/14 – 2014/15 was extensive and at its highest level since the mid-1990s (Figure 6.7), the areal extent of cold bottom water on the Grand Bank during spring spiked in 2014 and remained high in 2015 (Figure 6.7), the spring bloom has been delayed and relatively weak along most of the shelf (Figure 6.8), the abundance of *Calanus finmarchicus* has been low (Figure 6.9), and the 2015 Division 3L acoustic capelin survey index showed a slight decrease in biomass (Figure 6.10). Counter to negative trends in these temperate species, the first notable pulse of small snow crab in a decade has emerged (Figure 6.5). All inferences are that the recent cold years could slow the rebuilding process of cod and pace of transition along the NL shelf.

6.3.2 Unpredictable Future

Future climate is highly uncertain. The broadest spatial and temporal climate index of natural variability available upon which to draw inferences on the direction of ocean climate is the Atlantic Multi-decadal Oscillation, a mode of natural variability in sea surface temperatures occurring throughout the North Atlantic (Figure 5.12). As detailed in Chapter 5, it could be interpreted that the index has peaked and the coming decades will be cool, or it could be interpreted that the current warm phase will persist for another one to two decades before a transition back to a cool phase occurs.

Adding to uncertainties of the direction of the AMO are uncertainties associated with greenhouse gas loading into the atmosphere. The directional change in temperature from atmospheric carbon dioxide (CO_2) and other greenhouse gas loading is fairly certain, it will warm, but rates and patterns are debatable. The theoretical chemistry-based science of global warming is well advanced and is in a position to be proven wrong. The tests for its effects are largely biological, and may take considerable time to occur. However, two leading indicators, broad-scale land and sea surface temperatures, have increased virtually everywhere over the past two to three decades (IPCC, 2014).

It is known that the CO_2 presently being emitted will resonate in one of the major carbons sinks, the atmosphere, the land, or the oceans, for hundreds or thousands of years (Millero et al., 2009), and that CO_2 and other long-lived greenhouse gases create a blanketing effect for ultraviolet rays escaping the atmosphere. It is also known that earth has housed much higher levels of CO_2 and been much warmer in the past, albeit without man. The primary concern of

the current CO_2 loading is the rate of input, which is exceeding anything known before (Guinotte and Fabry, 2008; Kump et al., 2009). With concerns that land, atmospheric, and oceanic sinks are at or nearing their limits, and in some cases becoming net sources of carbon (Lenton, 2000; Sabine et al., 2004), the rate of input appears to be exceeding the rate at which earths ecosystems can naturally absorb the carbon. Further, in the oceans the solubility of CO_2 decreases with warming, thus the capacity of this integral carbon reservoir will diminish with global warming (Houghton, 2007).

Although rates and patterns of CO_2-forced warming are unknown, and short-term and small spatial-scale climate variability is unpredictable, some recent studies are predicting relatively rapid warming along the NL shelf in the coming decades. For example, Han et al. (2015) recently summarized that over the next 50 years projected sea surface and bottom temperatures off eastern Newfoundland will increase by about 0.4-2.2 °C and sea ice extent will decrease by 20-77 %.

An issue I struggle to reconcile is how natural variability associated with the AMO will associate with CO_2-forced warming. The time scale of warming of 50 years predicted by Han et al. (2015) and others directly overlaps with the AMO being in or largely having undertaken a cold phase. Will the natural signal of the AMO be lost, or conversely can our oceanic waters actually cool during global warming? Unfortunately, events to occur in the climate of the NL shelf ecosystem over the coming decades are unknown. The coming decades will undoubtedly be associated with change along the NL shelf, but in what direction and to what extent ultimately remains uncertain.

6.4 Application of the Research

Some aspects of the research presented herein are already being applied in management of the NL shelf fisheries. For example, the snow crab science has been effectively used to help control socio-economic outcomes of the resource decline. The temperature-induced prolonged productivity decline in snow crab has been thoroughly documented in recent stock assessments (Mullowney et al., 2015; DFO, 2016b) and communicated to industry. DFO management and communication sectors have publically featured the topic with an objective of preparing the fishing industry for forthcoming changes.

More broadly, some of the information contained herein has been used to inform industry stakeholders about an anticipated trophic control shift along the NL shelf. A DFO advisory document entitled 'Short-Term Stock Prospects for Cod, Crab and Shrimp in the Newfoundland and Labrador Region (Divisions 2J3KL)' (DFO, 2014) was produced while much of this research was being undertaken. However, preliminary insights were used alongside contributions from other researchers within DFO to help produce the document. That document ultimately serves as a communication piece to inform the industry about anticipated changes in the ecosystem.

Notwithstanding the information contained herein being used to communicate science to the industry and public, the results have not been formally implemented into an ecosystem-based fisheries management regime. Such a regime does not yet exist in NL. Nonetheless, despite lacking a model or formal process to synergistically amalgamate this information with other data on other species, DFO has started to consciously use such information in many of its stock assessments (i.e. DFO 2015a; DFO, 2016a;b). However, I anticipate that single-species

management approaches will prevail for the foreseeable future and the majority of this and other climate-based research into fisheries will continue to be used contextually as qualitative yardsticks for the outputs of quantitative assessment models. The benefits of moving beyond single-species assessment and management approaches are obvious, but the challenge of formally establishing true EBFM systems is monumental and the capacity to do so is not yet available. Nonetheless, my research will continue to be focused on climate and bottom-up processes in the ecosystem and I will continue my efforts to more formally implement them into assessment and management forums.

6.5 Perspectives on Unresolved Issues

The breadth of topics researched and discussed in this thesis is large, but it is far from an omniscient depiction of factors affecting the NL marine shelf ecosystem in recent decades. Debate continues within scientific and social realms on many aspects of finfish collapses and belaboured recovery. Two particularly contentious issues are whether or not predation by harp seals has been a key factor and whether or not the capelin stock actually collapsed.

Regarding harp seals, as shown in Fig. 1.7, their abundance quadrupled from the early 1980s to 2010. Some authors concluded they were the major predator in the post-collapse NL shelf ecosystem and exerted strong top-down control (Bundy 2001; Bundy et al., 2009) or even promoted depensation in cod populations via a 'predator pit' (Shelton and Healy, 1999). Stenson (2013) estimated only minor contributions of cod to the harp seal diet in offshore portions of Divisions 2J3KL during both winter and summer from 1986-2007. Even inshore, cod

made relatively minor contributions to the diet for most of the time series, however, notable increases in latter half of the 2000s occurred, particularly in Division 3L. Nonetheless, the existing consumption data do not suggest that direct mortality from harp seals was a major regulator of cod population dynamics. Beyond direct mortality from seal predation, indirect effects stemming from consumption of capelin and other forage fish could have affected cod (Bundy et al., 2009). Harp seals appear to select for capelin (Lawson et al., 1998), which is supported by direct diet observations showing that capelin dominates their diet in the offshore (Stenson, 2013). However, Stenson (2013) noted that total consumption of capelin and other prey by harp seals pales in comparison with predatory finfish in the NL Shelf ecosystem.

The most recent literature on the relative impacts of seal predation in regulating cod was from Buren et al. (2014). In a comprehensive suite of models, they found seal predation to be of minor importance relative to the effects of fishing and low capelin abundance in retarding cod recovery. Notwithstanding some impacts of seal predation on capelin, they concluded overall trophic control in the ecosystem was bottom-up, with the low abundance of capelin a critical limiting factor. My research, and ultimately my conclusions on the issue are in accordance with Buren et al. (2014). The NL shelf is at the southern extent of the harp seal range. It must be recognized that these predators spend only a small portion of their lives, generally in the order of about four months a year (i.e. from about late February to May when whelping and molting occurs) (DFO, 2000a), in the region.

Regarding capelin, a series of papers have suggested that the NL Shelf capelin stock did not collapse (Frank et al., 2013; 2016). Rather, the fish underwent changes in distribution to other parts of the Northwest Atlantic (Frank et al., 1996; Carscadden and Nakashima, 1997; Carscadden et al., 2001). Furthermore, largely following the decline in cod, a trophic cascade occurred along the NL Shelf characterized by overall increases in capelin and other pelagic fish in response to predation release (Frank et al. 2006; 2007).

There is strong evidence that capelin showed up in higher abundance in the warmer waters of the Eastern Scotian Shelf and Flemish Cap concomitant with stock collapse of cod and some other species (Frank et al., 1996). However, to suggest these increases can account for a loss of 6 million tons of capelin (Fig. 1.5, note it is an index) from the heart of its range in a single year is not fully rational. It is commonly known that some dense aggregations of capelin remained in some inshore bays following stock collapse (DFO 2000b; 2001). Particularly dense aggregations remained in Trinity and Placentia Bays (G.A. Rose, personal communication), where coincidentally cod groups were faring well. These observations are in keeping with a shift in distribution to the south (Frank et al. 1996) and also inshore. The capelin that spawned at a beach in Trinity Bay formed much of the basis for a multiplicative model (Evans and Nakashima, 2002) used for assessment of the stock in the years following collapse (DFO 2000b; 2001). I argue, in-line with Davoren and Montevecchi (2005) that this model was overloaded with redundant variables focused on a single remaining strong aggregation of capelin. The perception of the stock would have no doubt been radically different if the broader-scale

offshore acoustic data were not excluded or down-weighted in models used to assess capelin following the collapse.

MacCall's basin theory (MacCall, 1990) is a simple concept; fish can become densely aggregated in prime habitats when populations are low and 'spill-out' to other areas when populations are high. Over-interpretation of positive fishery and survey indices from hyper-aggregations occurred with the northern cod (Rose and Kulka, 1999) during stock collapse, as well as in the North Sea during collapse of that cod stock (Rice, 2006). Moreover, a similar phenomenon appears to be at-present occurring with the NL snow crab, with some areas experiencing increased or high catch rates while the stock is declining. My view is that conclusions that the NL Shelf capelin stock did not collapse have largely been based on over-interpretation of various indices associated with the few extant dense aggregations.

The importance of the issue of what is the most representative capelin data is high. For example, Buren et al. (2014) described how differences in outcomes on the importance of capelin in regulating cod during and after collapse between their modelling exercise and Bundy (2001) were largely attributable to the capelin data used to inform the models. Bundy (2001) used what I am describing as positively-biased indices on extant aggregations along with an offshore bottom trawl survey while Buren et al. (2014) used the offshore acoustic survey index. It must be noted that O'Driscoll et al. (2002) found that acoustic integration supported by directed trawling is the most representative method of surveying capelin, with the offshore bottom trawl survey unreliable. Similar acoustic methods have been used to survey capelin in Iceland and Norway for many years (Olafsdottir and Rose, 2012,2013; Gjøsæter et al., 2002b).

Thus, despite deficiencies, the offshore acoustic survey (Mowbray, 2014) is in my view the best method we currently have for assessing and interpreting capelin status.

Finally, regarding the contention that the capelin stock did not collapse and more broadly that a trophic cascade occurred in the NL Shelf ecosystem, this conclusion hinges on establishing a strong negative relationship between predators and prey (Frank et al., 2006,2007). This has simply not been the case in this ecosystem, with the relationship between cod and capelin, the dominant predator and prey species in the region, very strong for the past two decades (Fig. 6.11). As stated throughout this thesis, capelin are critical to the success of cod in the NL Shelf marine ecosystem.

6.6 Conclusions

I conclude that warming is having a profound impact on the Newfoundland and Labrador shelf ecosystem acting both directly and indirectly on important commercial species. Climatic phenomena exert a high level of influence over lower trophic level processes and their impacts resonate throughout the foodweb of the NL shelf and ultimately affect the fisheries.

Overall, it is apparent that the NL shelf is in a transitional phase, shifting from a bottom-up controlled ecosystem toward one more top-down structured. The level and rate of transition potentially forthcoming is unknown, but changes are not likely to be as rapid or substantial as the late 1980s / early 1990s regime shift. However, if the forage base of capelin continues to improve and fisheries do not prematurely interfere with rebuilding finfish stocks, the next decade will likely constitute the most pronounced shift in trophic control since stock collapses.

The ecosystem is transitioning largely due to a warming in the climate system over the past 20 years. This transition has no doubt been influenced by the changes in fishing patterns from cod to crustaceans. Nonetheless, the underlying rationale on why the ecosystem is transitioning is that food-limitation throughout the foodweb is easing and overall trophic throughput in the system is increasing. Capelin have benefitted from improved access to zooplankton, and cod have benefitted from improved access to capelin. Above all else, the extent to which capelin re-establishes itself will likely determine the forthcoming state of the ecosystem.

Converse to capelin and cod, snow crab productivity has been directly and negatively affected by increasing temperatures and this stock is likely to decline further in the coming decade. It is anticipated that the fisheries of the coming decade will need to diversify more toward temperate finfishes and place less emphasis on cold-water crustaceans. However, fishery removals from cod and capelin are advised to remain low in the short-term to allow for more of the recovery potential of the stocks to occur over the long-term.

Short-term climatic variability is creating instability in the rebuilding process of finfish and uncertainty in the extent to which the present trophic control shift will occur. Long-term climate outcomes, and consequently ecosystem productivity outcomes, are unknown.

The scenario being presented, with declines in the snow crab resource and rebuilding finfish populations not yet able to withstand high levels of fishery prosecution is undoubtedly a challenging one for industry stakeholders and managers, particularly in light of tough economic times. However, from an ecological perspective, this is clearly a time to be cautious in

management. This situation will test the collective resolve of all industry stakeholders to practice restraint in the true spirit of ecosystem-based fisheries management.

6.7 References

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6.8. Figures

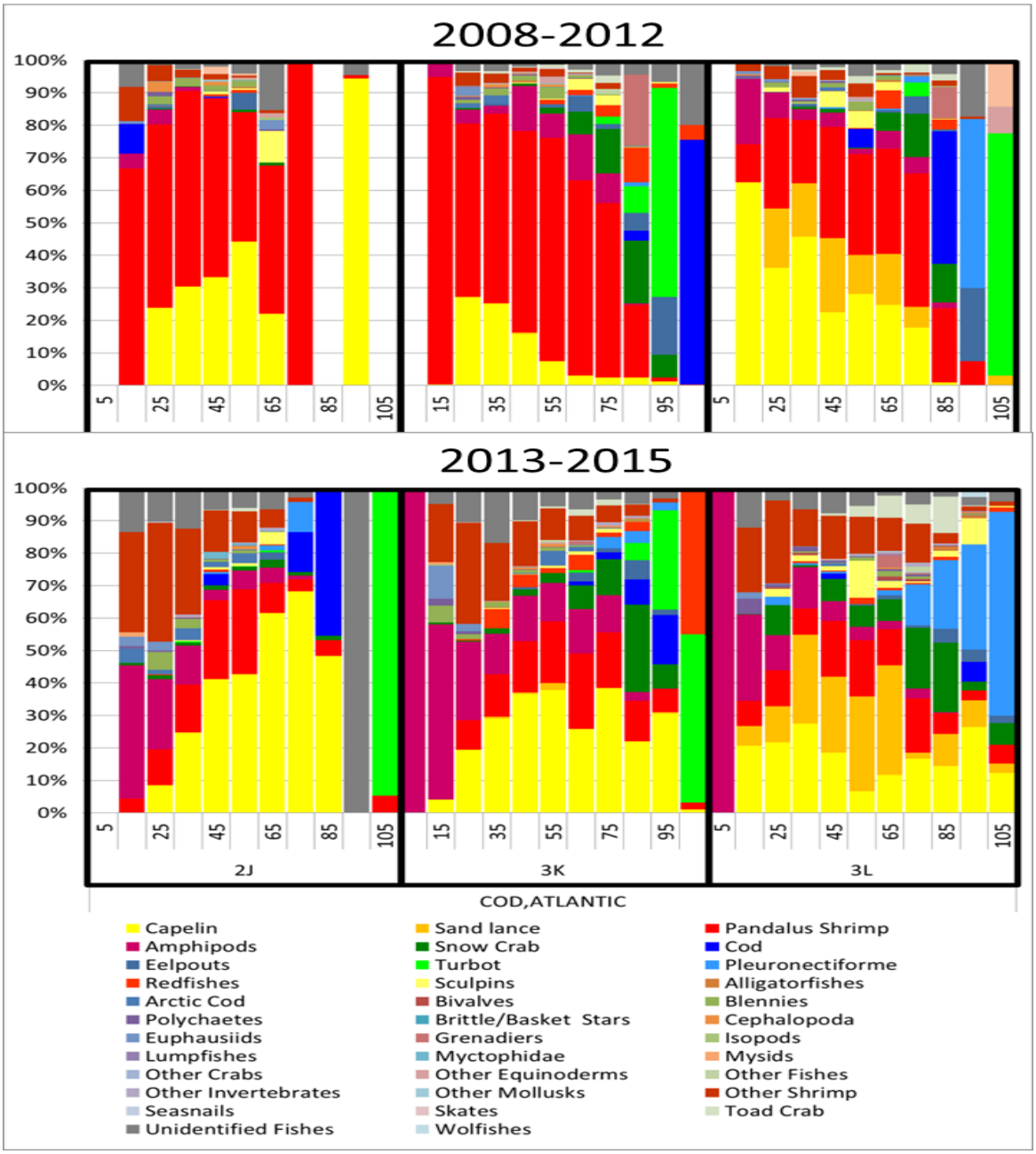

Figure 6.1. Northern cod diet in Divisions 2J3KL from 2008-2013. Data are from fall trawl surveys. X-axis in each panel depicts cod size groups (total length). Capelin in bright yellow and pandalid shrimp in bright red. Ordinate value is percentage of the diet by weight for each species. Figure provided by Mariano Koen Alonso, DFO.

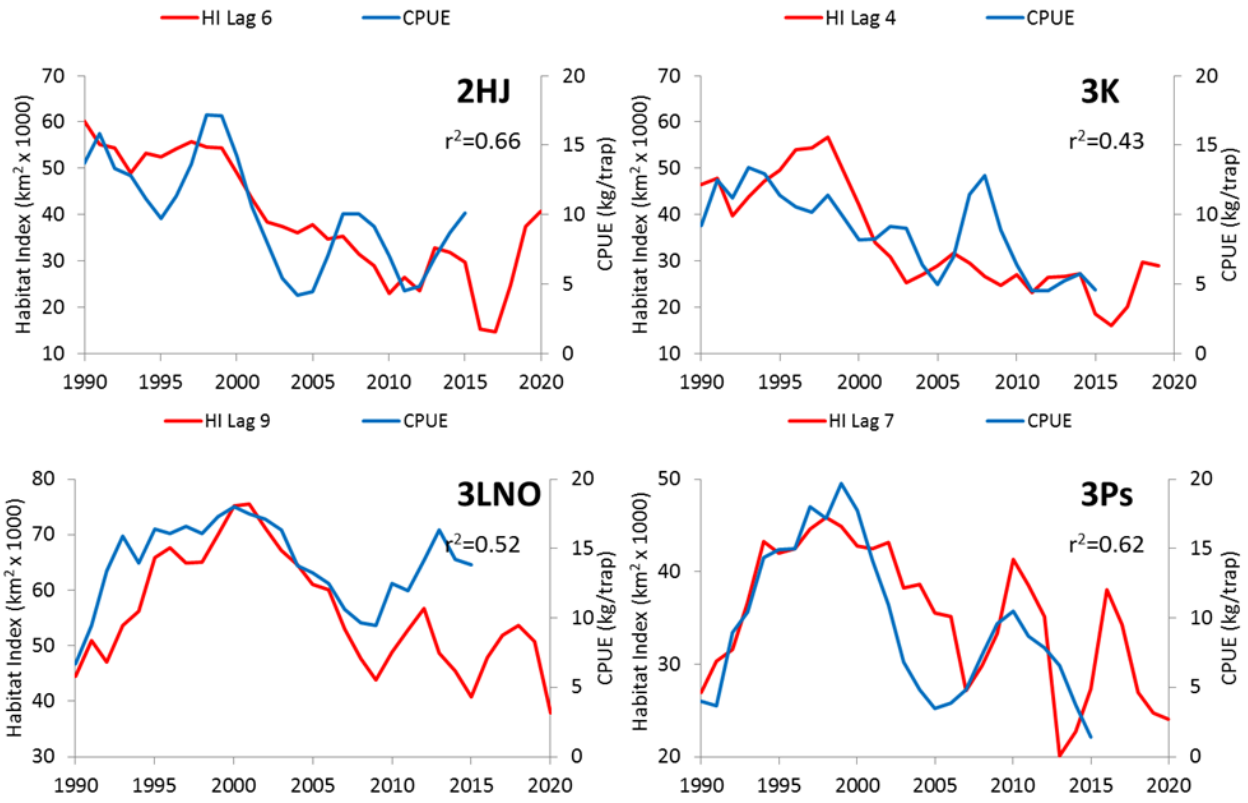

Figure 6.2. Snow crab thermal habitat indices (HI) versus fishery catch per unit of effort (CPUE) by assessment division for Newfoundland and Labrador snow crab. Habitat indices defined as the areal extent of cold bottom water (<2°C in Divs. 2HJ, 3K, and <1°C in Divs. 3LNO, 3Ps), with samples taken from multi-species trawl surveys. Habitat indices lagged against CPUE at best fit lags.

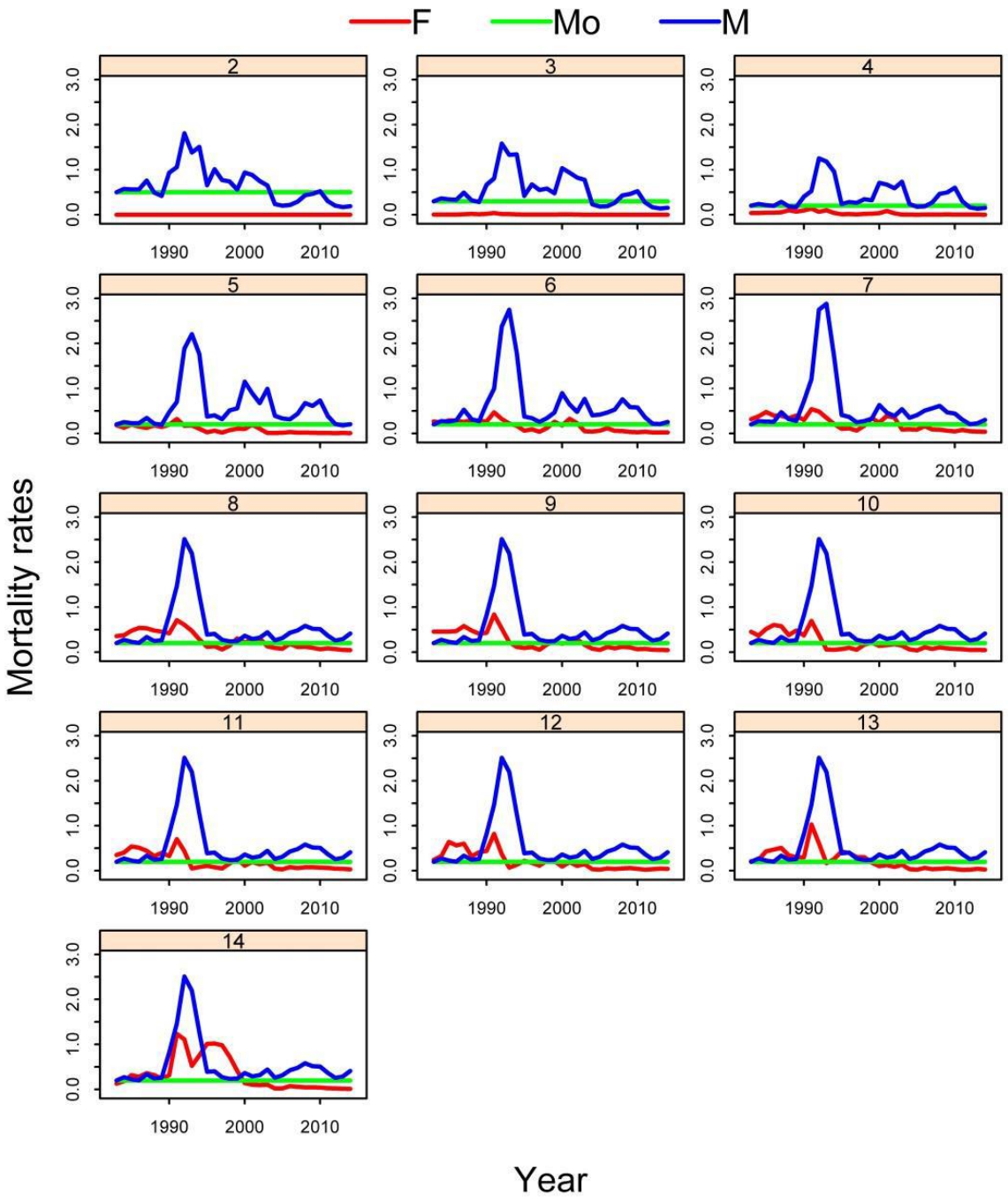

Figure 6.3. Mortality rate at age estimates from the NCAM model. F denotes fisheries-induced mortality rate, M denotes natural mortality rate, and Mo shows the fixed mean values of M. Figure taken from Cadigan, 2016b.

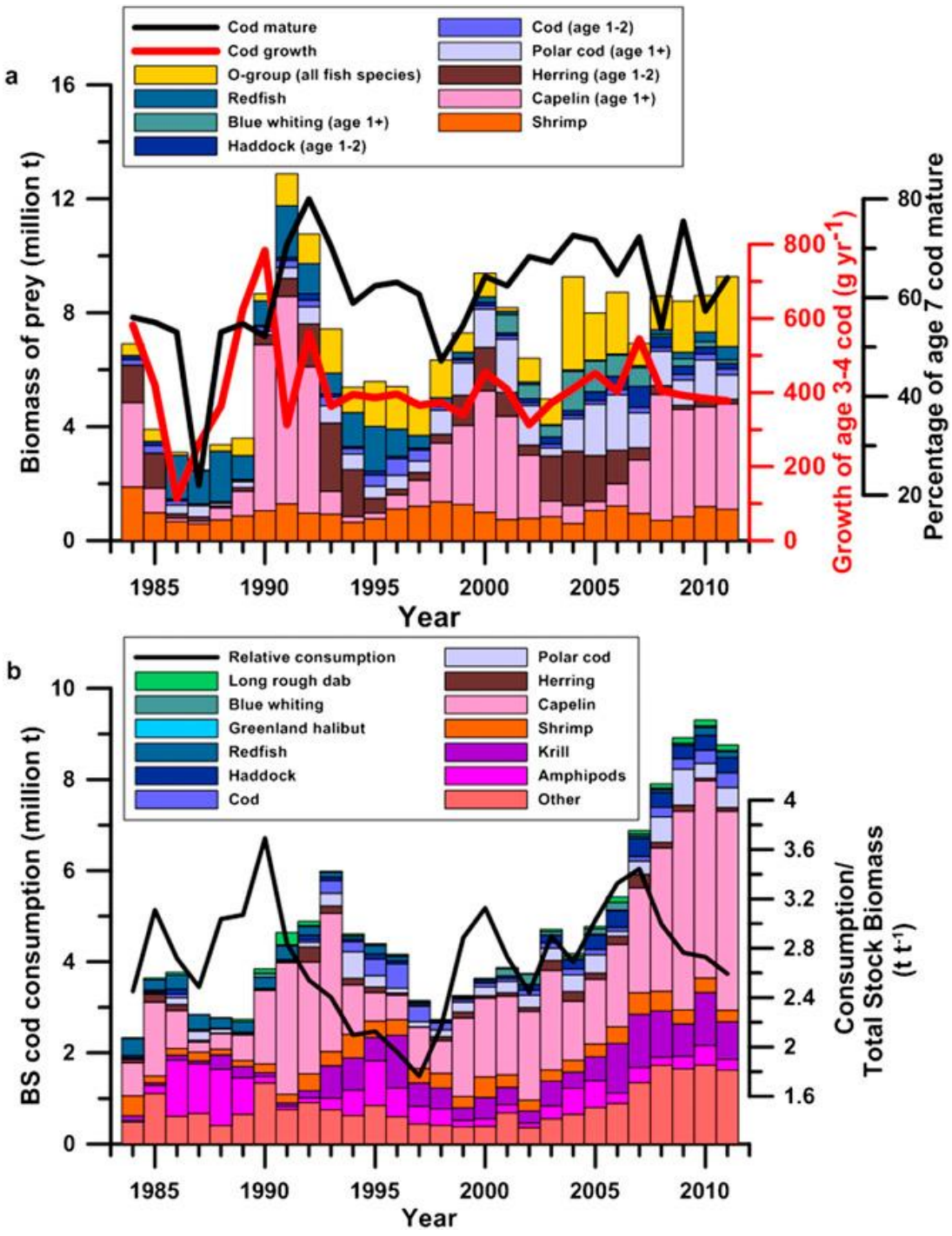

Figure 6.4. Prey abundance and consumption of Northeast Arctic cod and associated growth and maturation dynamics. Top panel (a) shows biomass of main prey items, growth from ages 3-4, and the percentage of fish mature at age 7. Bottom panel (b) shows estimated total and relative consumption. Relative consumption estimated as total consumption / total biomass of age 2+ cod. Figure taken from Kjesbu et al., 2014.

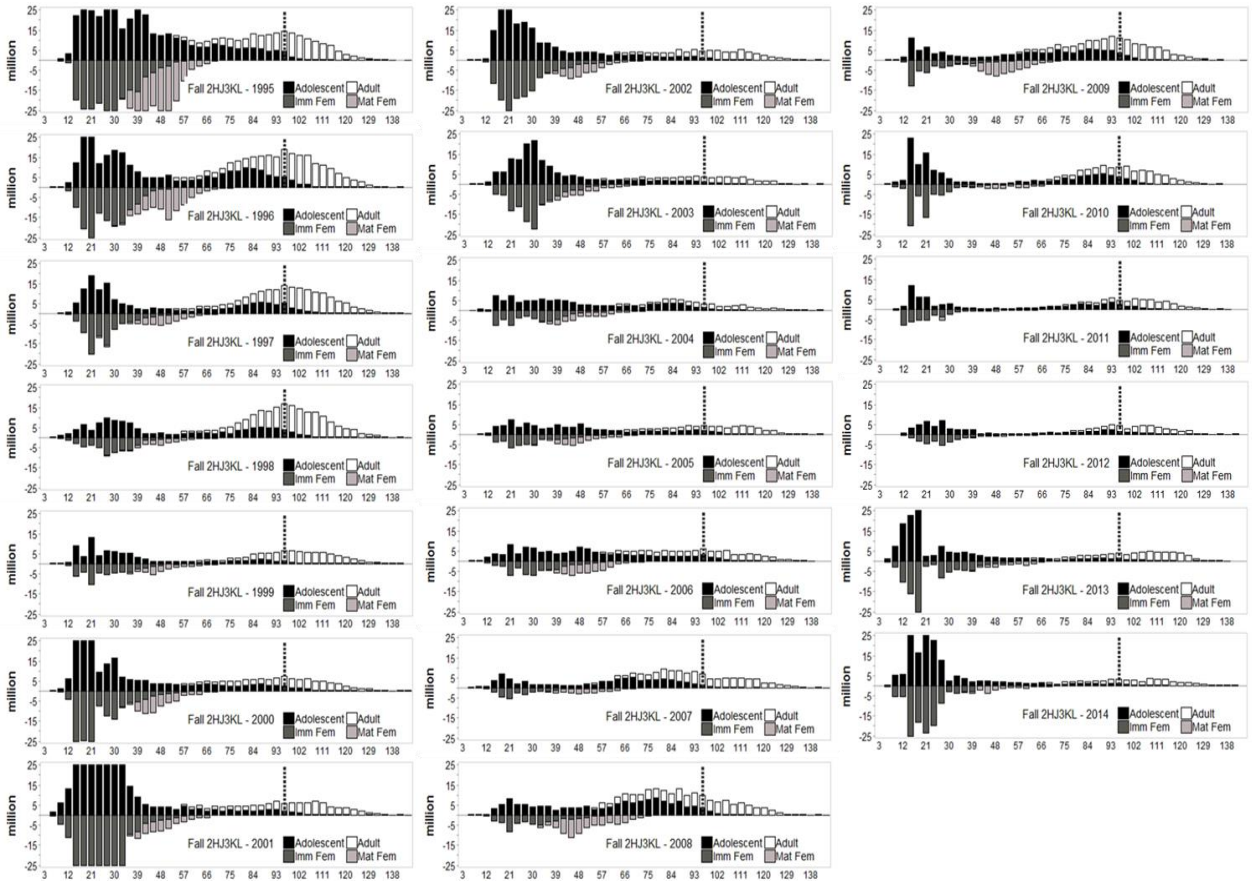

Figure 6.5. Annual abundance indices of male and female snow crab by size from Divisions 2HJ3KL fall trawl surveys. Adolescent males in black and adult males in white. Immature females in dark grey and mature females in light grey. X-axis units are carapace width (CW).

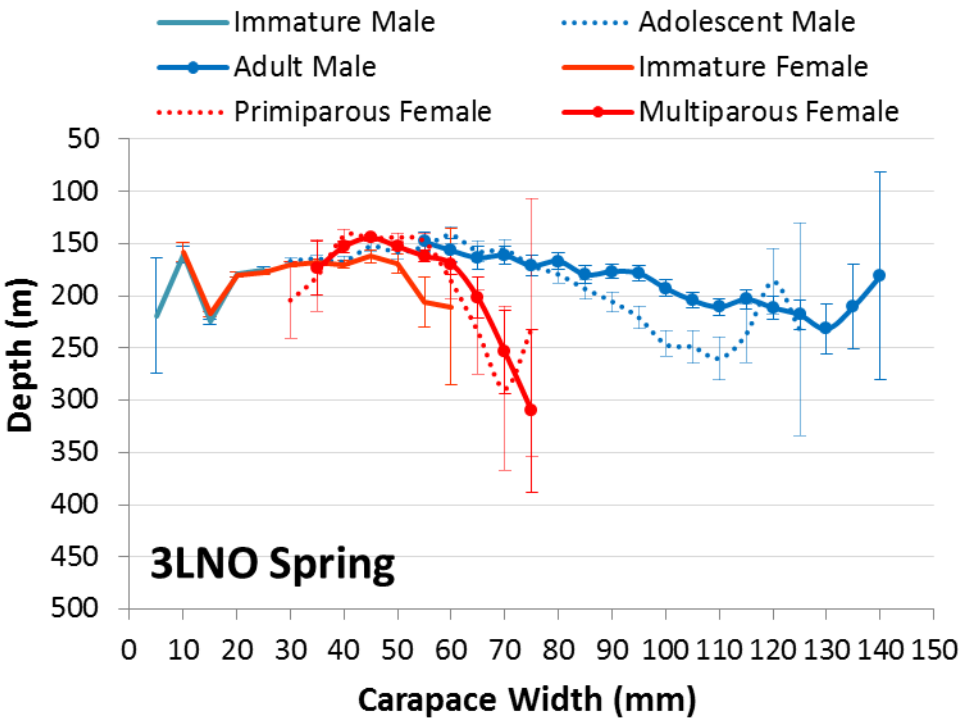

Figure 6.6. Average depth by size and mating status for snow crab captured in spring multi-species trawl surveys in NAFO Divisions 3LNO from 1996-2015. Error bars represent 95% confidence intervals.

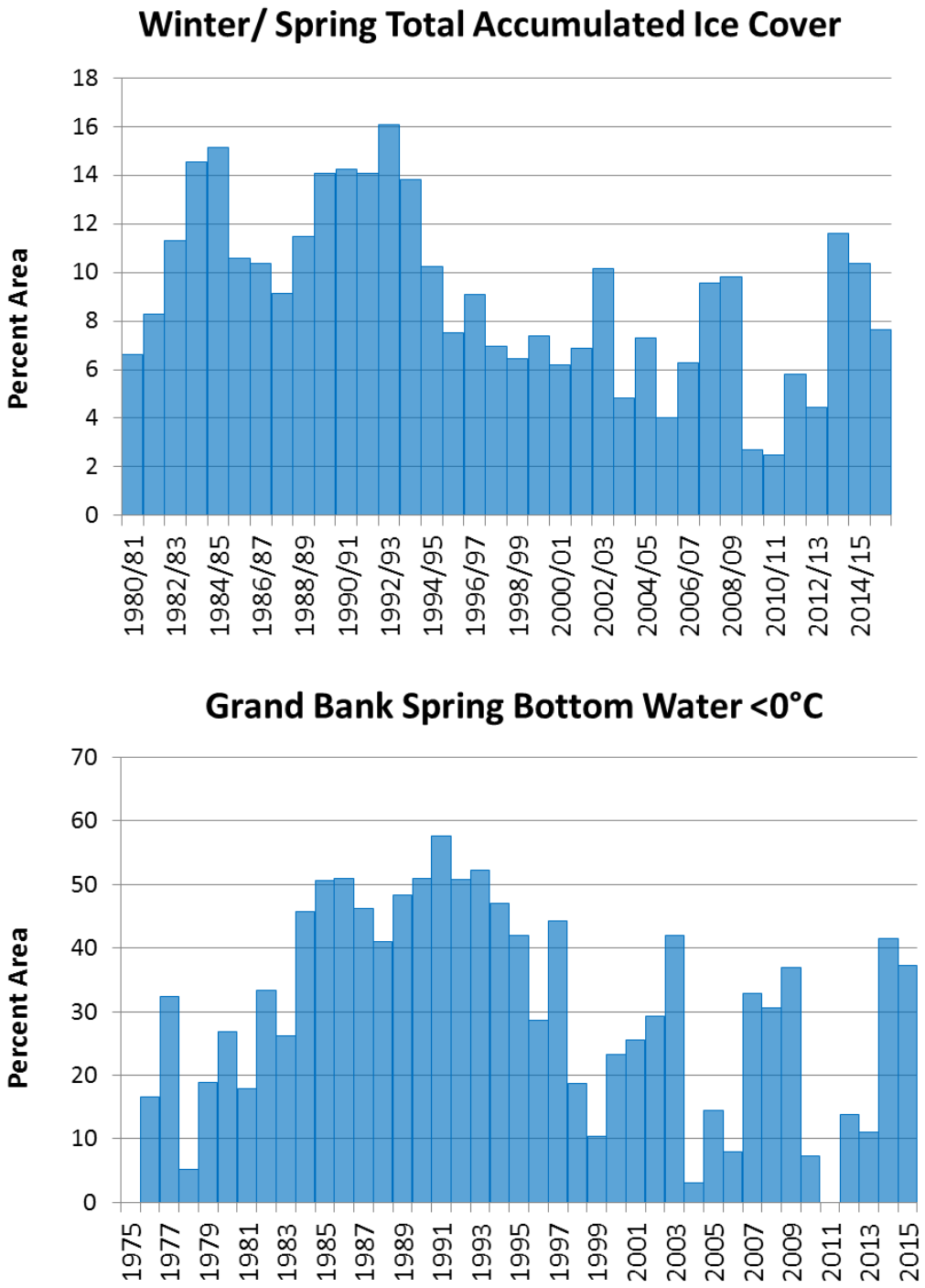

Figure 6.7. Top panel - Total accumulated ice cover from Nov. 12 – June 4 in Atlantic Canada each year from 1980-2016. Index is percent coverage of sea surface area in the region. Ice data acquired from Environment Canada (http://iceweb1.cis.ec.gc.ca/Prod/page3.xhtml). Bottom panel – Percentage of Div. 3LNO bottom covered by <0°C water during spring surveys from 1976-2015. Data property of DFO.

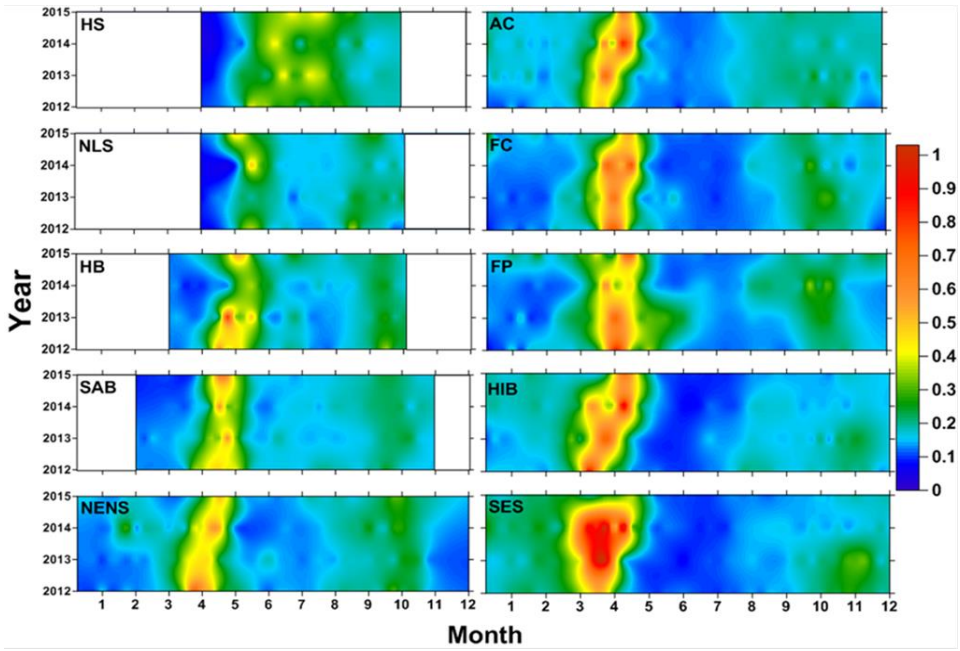

Figure 6.8. Satellite-based surface chlorophyll a concentrations from Petrie Box locations along the NL shelf from 2012-2015 (North to South: HS=Hudson Strait, NLS=Northern Labrador Shelf, HB=Hamilton Bank, SAB=St. Anthony Basin, NENS= Northeast Newfoundland Shelf, AC=Avalon Channel, FC=Flemish Cap, FP=Flemish Pass, HIB=Hibernia, SES=Southeast Shoal). Figure provided by Gary Maillet, DFO.

Calanus finmarchicus	**1999**	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**	**2007**	**2008**	**2009**	**2010**	**2011**	**2012**	**2013**	**2014**	**2015**
Seal Island	0.1	-2.0	-0.7	0.1	0.2	1.4	1.2	0.4	0.5	0.0	-1.6	0.4	1.0	0.2	0.2	-1.0	-0.9
Bonavista	-1.9	-1.9	-0.2	0.1	0.2	1.0	0.1	1.4	0.7	0.0	0.1	0.4	0.0	0.3	1.1	-0.7	-1.1
S27	1.1	0.4	0.1	0.5	0.0	-0.7	0.0	-0.2	-0.1	-2.7	0.3	1.3	0.5	-0.5	-1.9	0.3	-1.1
Flemish Cap	-1.0	-2.5	0.6	0.7	0.0	-0.2	0.5	1.1	-0.2	0.1	-0.1	1.1	1.1	1.3	0.0	-0.6	0.5
SE Grand Banks	-2.4	-1.5	0.2	0.7	0.5	0.0	0.8	0.0	0.2	0.0	0.6	0.8	1.1	0.3	0.4	-0.3	-1.2
***Pseudocalanus* spp.**																	
Seal Island	0.0	-0.5	0.2	-0.6	0.2	-0.3	-0.7	0.7	1.6	1.5	-2.1	-0.2	0.8	1.8	-0.8	0.0	2.2
Bonavista	-1.2	-1.8	1.1	0.0	0.5	0.0	-1.0	0.6	-0.5	-0.1	0.9	1.5	-0.6	-0.1	2.8	2.3	1.4
S27	-0.6	0.8	0.3	0.5	0.3	-1.7	-0.2	-0.8	0.5	-1.5	1.7	0.8	0.2	0.2	0.7	1.8	1.9
Flemish Cap	-0.2	1.5	-0.3	1.5	-0.5	-0.8	-1.4	0.0	-0.7	-0.6	-0.1	1.7	-1.6	-0.3	3.4	4.3	6.0
SE Grand Banks	-2.5	1.2	0.5	0.8	-0.7	-0.1	0.7	-0.6	0.5	-0.6	0.0	0.7	1.4	-0.6	1.5	2.1	0.8
Copepods																	
Seal Island	-0.9	-1.9	-0.8	0.0	0.4	1.5	1.2	1.3	0.2	-0.4	-0.6	0.0	0.0	-0.9	0.2	-1.1	-0.5
Bonavista	-1.8	-1.7	-0.4	-0.7	0.4	0.3	-0.3	1.2	0.5	0.4	0.8	1.1	0.1	-1.2	1.5	-0.1	0.4
S27	-0.5	0.3	-0.5	0.5	0.1	-1.1	-0.1	-1.3	0.5	-1.2	2.1	1.2	1.1	-0.3	0.0	2.3	1.8
Flemish Cap	-1.4	-1.3	0.0	-0.4	-0.9	-0.5	0.4	1.1	0.2	0.4	0.5	2.0	0.2	0.8	0.7	0.1	1.9
SE Grand Banks	-2.5	0.4	-1.1	-0.1	-0.1	0.1	1.0	-0.3	0.8	0.1	0.9	1.0	1.6	1.1	-0.2	0.2	0.7
Non-copepods																	
Seal Island	-1.6	-0.7	-0.2	-0.7	-0.1	1.2	1.0	2.0	0.1	-1.0	-0.1	0.2	0.1	-1.0	0.7	-0.3	1.0
Bonavista	-1.5	-1.9	0.2	0.1	0.3	-0.3	-0.1	1.6	0.0	-0.3	1.1	1.1	-0.4	-0.6	1.8	0.0	0.6
S27	-0.5	0.3	-0.5	0.5	0.1	-1.1	-0.1	-1.3	0.5	-1.2	2.1	1.2	1.1	-0.3	0.0	2.3	1.8
Flemish Cap	-2.0	0.1	0.4	0.7	-0.8	-0.8	0.0	0.3	-0.4	0.2	0.1	2.2	0.6	1.9	2.6	2.0	2.5
SE Grand Banks	-2.5	1.5	0.4	0.1	-0.1	-0.5	0.5	0.0	-0.5	-0.1	0.0	1.3	0.5	1.2	0.4	0.8	-0.4

Figure 6.9. Standardized anomalies of key zooplankton species along transect lines occupied by spring oceanographic surveys along the Newfoundland and Labrador shelf from 1999-2015. Anomalies were calculated based on the 1999-2010 average. Figure provided by Gary Maillet, DFO.

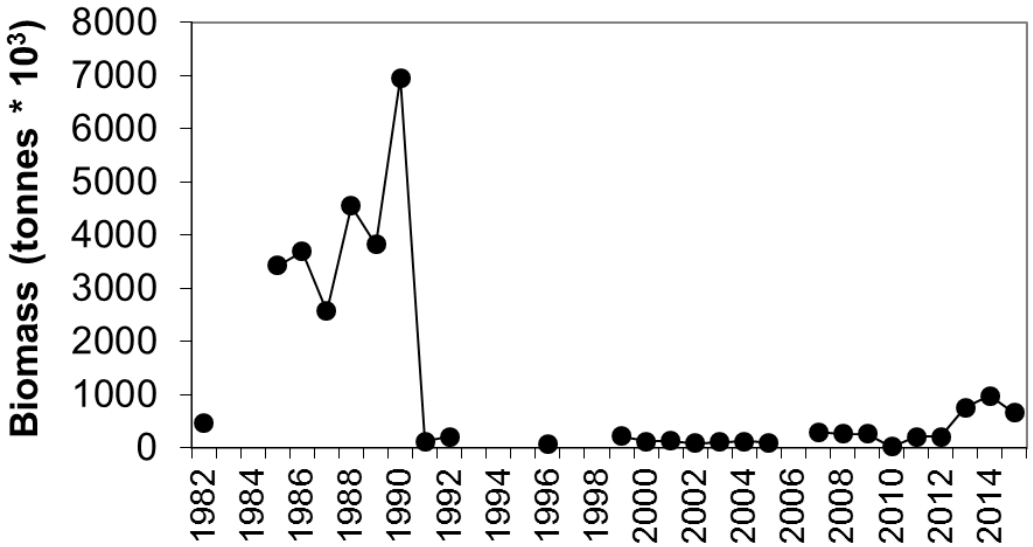

Figure 6.10. Capelin Acoustic Biomass Index from the DFO spring capelin survey in NAFO Divisions 3KL. Figure provided by Fran Mowbray, DFO.

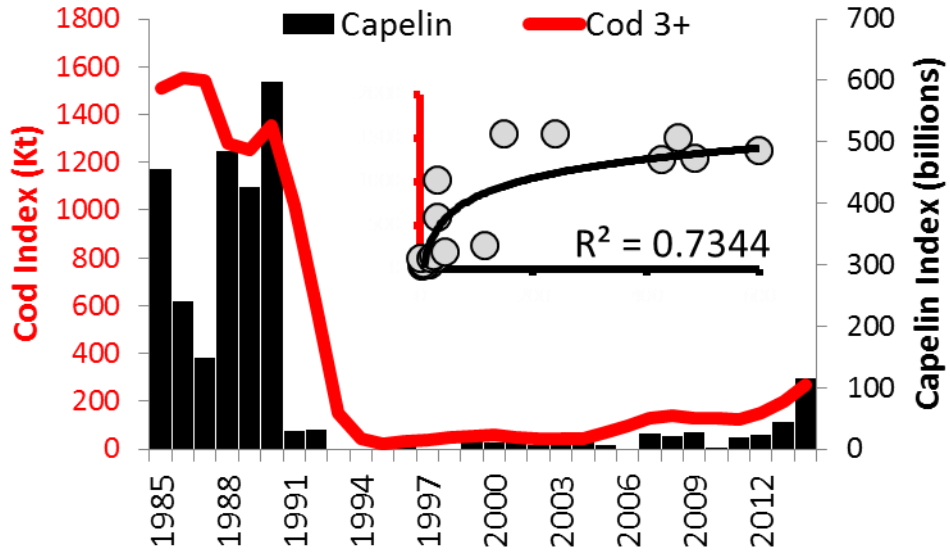

Figure 6.11. Biomass estimates for ages 3+ cod (taken from Cadigan, 2016b) and capelin abundance (estimated from DFO, 2014) from 1985 to 2014 and their relationship.